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Life Cycle of *Steinernema scapterisci* Nguyen & Smart, 1990[1]

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Abstract: The life cycle of *Steinernema scapterisci* Nguyen and Smart, 1990 consists of an egg stage, four juvenile stages, and an adult stage (male and female). The cycle from IJ (third stage infective juveniles) to IJ may proceed by one of two routes. If the nutrient supply is sufficient and the population is not overcrowded, the IJ develop to adult males and females of the first generation. Most eggs from these adult females hatch and the juveniles develop through each life stage to become adult males and females of the second generation. Eggs produced by these females develop to IJ. This cycle takes 8–10 days (long cycle) at 24 C. If the nutrient supply is insufficient or if overcrowded, the IJ develop to adult males and females of the first generation, and eggs produced by the females develop directly to IJ. This cycle takes 6–7 days (short cycle). The nematode is less tolerant of lower temperatures and more tolerant of higher temperatures than are other species of the genus. The sex ratio is influenced by temperature. At 15 and 24 C, females constituted 54% and 60% of the population, respectively, but at 30 C females constituted 47% of the population.

Key words: entomopathogenic nematode, life cycle, nematode, sex ratio, *Steinernema scapterisci.*

The life cycle of species in the genus *Steinernema* Travassos, 1927 (=*Neoaplectana* Steiner, 1929) as described by previous researchers (1,3,4,10) consists of an egg stage, four juvenile stages, and an adult stage (males and females). The J2 (second-stage juvenile) may be the preinfective stage or the non-preinfective stage, and the J3 (third-stage juvenile) may be the infective stage or the noninfective stage. Generally two complete generations occur in an insect host. Most researchers agree that some of the eggs produced by the first-generation females develop into IJ (infective J3), but the majority of the eggs develop into second-generation adults. The eggs produced by the second-generation females develop into IJ. Wouts (12) presented an updated life cycle and a redescription of *S. bibionis* Bovien, 1937. He reported that in a fresh host with a low population density, the J1 (first-stage juvenile) developed directly to the J4 (fourth-stage juvenile) without going through the J2 and J3 stages. When the population density increased, however, the J1 developed to J2 and then to IJ.

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This investigation reports on the life cycle of *S. scapterisci* (8), including the influence of temperature on the life cycle and the sex ratio.

Materials and Methods

Mole crickets, *Scapteriscus borelli* Giglio-Tos (formerly *Scapteriscus acletus* Rehn and Hebard), and house crickets, *Acheta domesticus* L., were used; they are equally good hosts for the nematode (9). The mole crickets were collected from the field or reared in the laboratory, and the house crickets were purchased from a local bait shop.

Life cycle: The life cycle was studied at 24 C by exposing crickets to 8,000 IJ in a petri dish (100 × 15 mm) lined with moistened filter paper, and then dissecting crickets daily until the life cycle of the nematode was completed. One cricket was dissected on a schedule of 6, 6, and 12 hours after exposure. Each cricket was dissected in a petri dish (60 × 15 mm) in 0.1 ml water. The body fluids of the cricket mixed with the water and provided a suitable medium for development of the bacterium and nematode. Between observation periods, the petri dish lids were applied and each dish was stored in a large petri dish (150 × 25 mm) containing a filter paper kept wet at all times. The process of infection and dissection was replicated up to 10 times to

confirm the presence of each life stage and to follow the development of certain structures. If the crickets were alive at the appointed hour for dissection, they were anesthetized with CO_2 and dissected immediately. Nematodes dissected from the crickets were observed approximately every 15 minutes for up to 8 hours the first day and again the next day until either they molted to the next stage or 32 hours had elapsed. Each life stage is distinct and can be identified morphologically.

Short life cycle: Preliminary studies (7) indicated that, when overcrowded or when the food supply was limited, *S scapterisci,* like other Steinernematidae, has a short life cycle (eggs from first-generation females develop into IJ) in addition to the normal (long) cycle (eggs from first-generation females develop into second-generation adults and eggs from those females develop into IJ). To confirm the presence of a short cycle, 50 house crickets were exposed to 8,000 IJ as described above and kept at 24 C. Crickets were dissected daily until adult males and females were detected. At that time, a small piece of tissue from the thorax (ca. 1 mm^3) of an infected cricket was placed on a small piece of water-saturated filter paper (1 cm^2) in a petri dish (60 × 15 mm). Any nematodes on the tissue were removed, and two preadult females and two adult males taken from the same insect were placed on the tissue. Four drops of water were placed in the petri dish surrounding the filter paper to insure adequate moisture, and the lid was applied. There were 20 replicates. All dishes were placed in plastic bags containing paper toweling saturated with water. The bags were tied and kept in the dark at 24 C. The dishes were examined daily. After 7 days, the experiment was terminated and nematodes counted.

Influence of temperature on the life cycle: To determine the influence of temperature on the life cycle, house crickets were anesthetized with CO_2 and placed 50/dish in each of 16 petri dishes (100 × 15 mm) and exposed to 8,000 IJ. Two of the petri dishes were placed in incubation chambers at 10, 15, 20, 24, 30, 33, 35, and 37 C. After 2 days, 1–3 crickets were dissected daily, and the life stages of the nematode determined.

Influence of temperature on sex ratio of first-generation adults: To determine the influence of temperature on the female/male sex ratio, 10–12 house crickets were placed in each of three petri dishes and exposed to 8,000 IJ. One of the dishes was placed in an incubator at 15, 24, and 30 C. After 3 days, all crickets were dissected and the number of females and males in each cricket was counted. The female/male ratio was analyzed with Duncan's multiple-range test and linear regression using SAS (11).

Results

Life cycle: The life cycle of *S. scapterisci* is composed of both a long and a short cycle (Fig. 1).

Long (normal) cycle: The IJ invade the host through the mouth or spiracles, penetrate into the hemocoel, and accumulate in the thorax and head. The body of the IJ becomes wider, the stoma opens, and its walls thicken. The esophagus becomes prominent. The bacterial chamber (Fig. 3L) in the anterior region of the intestine enlarges and the bacteria move posteriorly until they are released through the anus into the hemocoel of the host. This process takes less than 24 hours after the IJ enter the host. The IJ now become feeding J3 and feed on the multiplying bacterial cells and grow rapidly before molting to the J4. The body width of the J4 increases much faster than does its length, until it becomes almost as wide as the adult. Then its length increases until it becomes as long as the adult. During this time, the excretory duct becomes larger and more complicated structurally, and the reproductive system is formed. Then the J4 molt to the first-generation adult males and females in 60–72 hours after entering the host. These adults mate and the female lays eggs initially, but later the eggs are retained and hatch in her body. Some 12–24 hours later, the J1 break out of her body and move into the hemocoel of the insect.

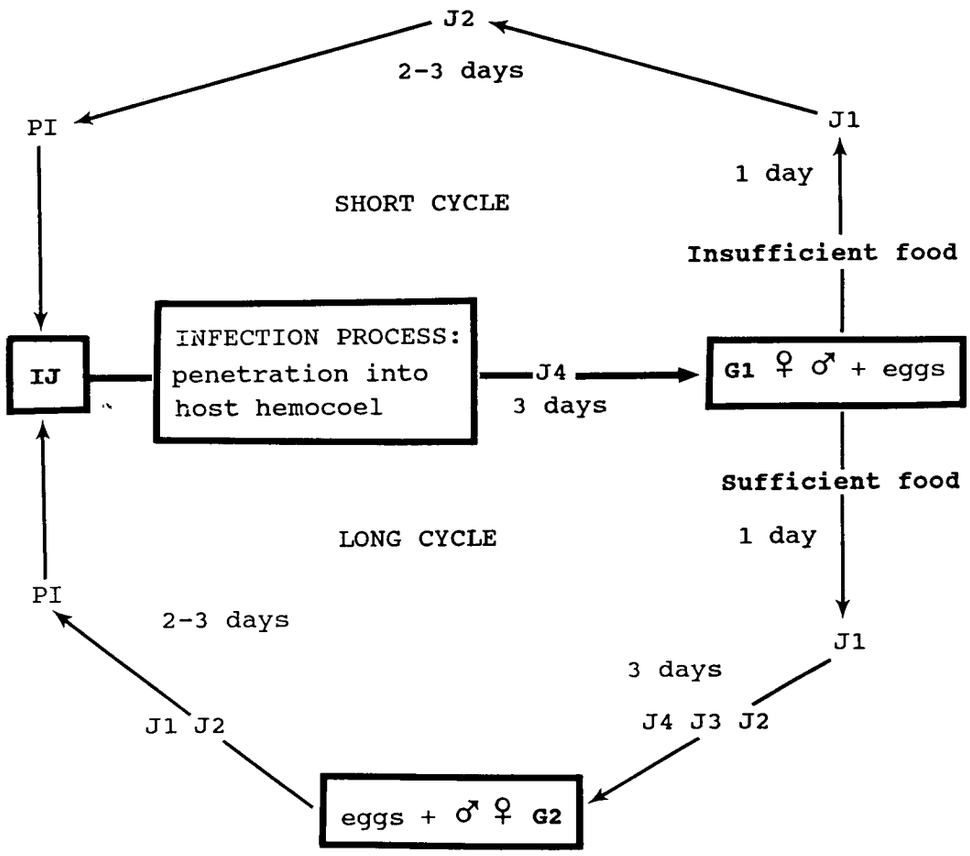

FIG. 1. Diagram of the life cycle of *Steinernema scapterisci*. G1 = first-generation adults, G2 = second-generation adults, J1 = first-stage juvenile, J2 = second-stage juvenile that may be the preinfective or non-preinfective stage, J3 = third-stage noninfective juvenile, PI = preinfective stage, IJ = third-stage infective juvenile, J4 = fourth-stage juvenile.

Some of the J1 molt to the J2, which later become preinfective J2 and molt to the IJ (infective J3), retaining the cuticle of the J2 as a sheath. Other J1 undergo successive molts to the J2, the noninfective J3, the J4, and second-generation adult males and females. Second-generation adults are much smaller than first-generation adults. The females of the second generation lay some eggs initially, but most are retained and hatch in her body. These second-generation J1 molt to the preinfective J2, which molt to the IJ retaining the cuticle of the J2 as a sheath. The IJ leave the insect cadaver and seek out new hosts.

Short cycle: On a small piece of tissue, J3 were first observed 6 days after the pre-adult females and adult males were placed on the tissue; many J3 were present after 7 days. About 98% (347 ± 217; range 103–913) of these J3 were IJ, and 2% (7 ± 10; range 0–41) were noninfective J3. In 6 of the 20 replicates, all of the J3 were IJ and in 5 others, more than 99% were IJ. The IJ produced by the short cycle were equally as infective to house crickets as those produced by the long cycle. The average reproductive rate of a first-generation female was 177 (n = 20, range 53–457) J3.

Description of the life stages

First-stage juvenile (J1): The J1 emerges from the egg. The body from head to anus is almost cylindrical, but tapers from the anus to the tail. The length ranges from 289 μm to 525 μm and the width from 18

μm to 24 μm (n = 10). The body is greenish-yellow with several dark areas (dots) scattered throughout. Later, the body becomes darker in color and tapers at both ends. Labial papillae are prominent (Fig. 2A). The stoma is funnel-shaped and comprises two short cylindrical rings, which in lateral view appear as two sclerotized structures (Fig. 2A). The basal bulb of the esophagus, which is almost as wide as the pseudocoelom, possesses a prominent valve (Fig. 3J). The lumen of the intestine is large and prominent initially, but as the nematode grows, its diameter, except near

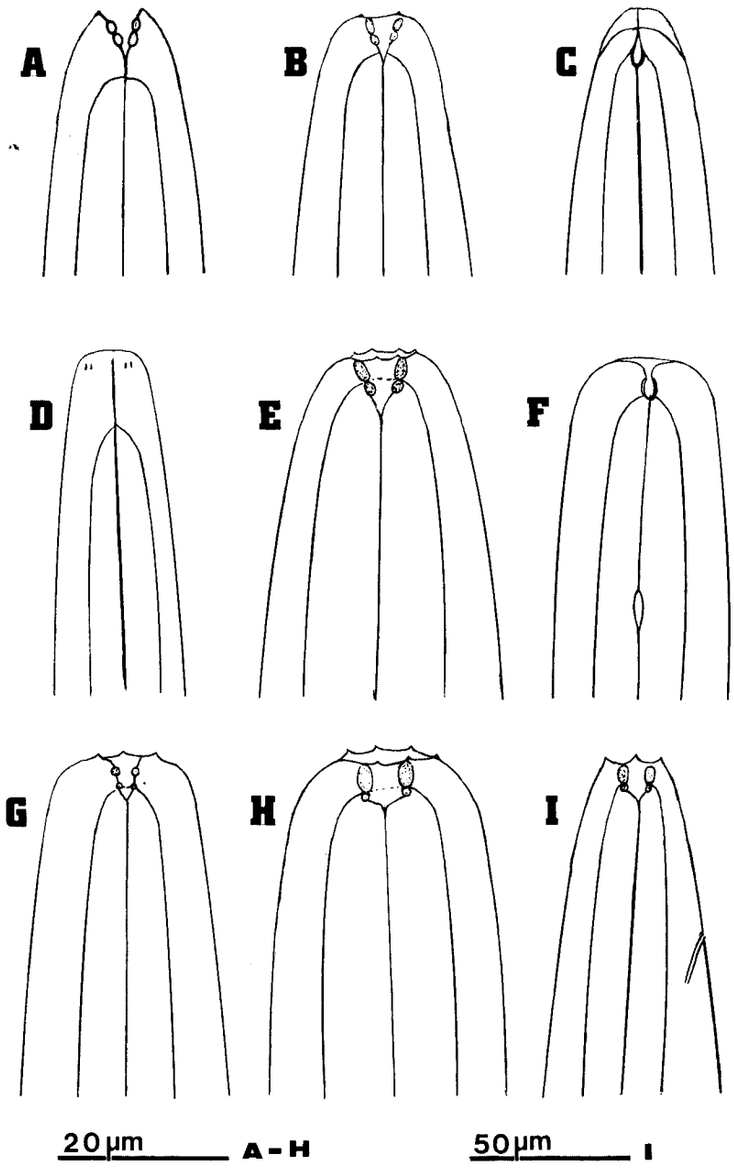

FIG. 2. Head regions of different stages of *Steinernema scapterisci*. A) First-stage juvenile. B) Second-stage juvenile. C) Preinfective second-stage juvenile. D) Infective stage juvenile. E) Feeding third-stage juvenile. F,G,H) Different steps of development of the infective juvenile to the feeding third-stage juvenile of the first generation. I) Fourth-stage juvenile.

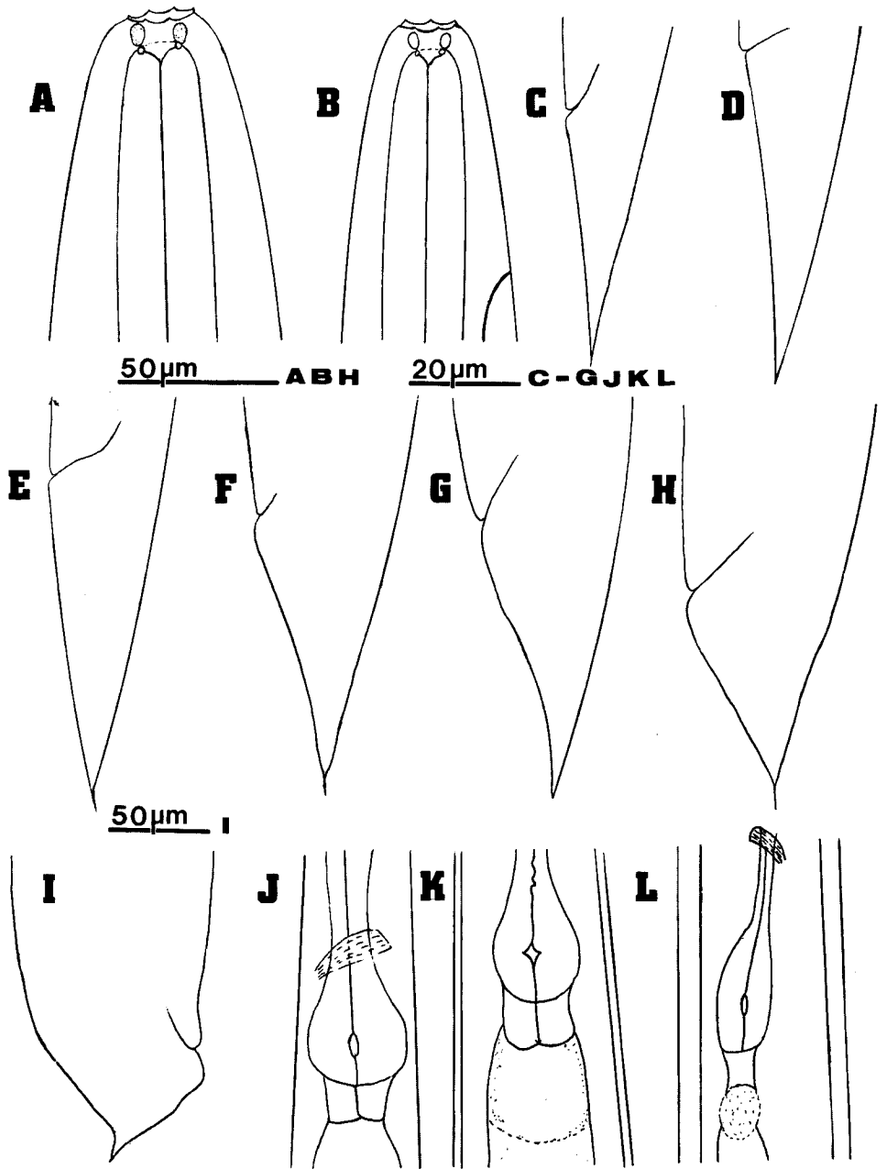

FIG. 3. Different structures of *Steinernema scapterisci*. A) Head region of first-generation female. B) Head region of second-generation female. C) Tail of first-stage juvenile. D) Tail of second-stage juvenile. E) Tail of preinfective second-stage juvenile. F,G) Tails of feeding third-stage juveniles. H) Tail of second-generation female. I) Tail of first-generation female. J) Basal bulb of esophagus of first-stage juvenile. K) Basal bulb of esophagus and bacterial chamber forming in the intestine of the preinfective second-stage juvenile. L) Basal bulb of esophagus and bacterial chamber in the intestine of the infective stage juvenile.

the base of the esophagus, becomes smaller and appears thread-like just before molting. The J1 molts to the J2 about 12 hours after hatching. J1 dissected from a mole cricket and placed in water die without further development. We believe that the J1 does not feed.

Second-stage juvenile (J2): The body of the J2 is dark and tapered at both ends. The length ranges from 500 µm to 669 µm

and the width from 30 μm to 48 μm (n = 10). Labial papillae are distinct but not as prominent as in the J1. The stoma is large and bears two thick, dark structures on each side (Fig. 2B). If food is sufficient, the J2 develop to the J3 (Fig. 2E). If food is insufficient, or if the J2 are removed from a food source, after about 12 hours the stoma narrows, the esophagus becomes reduced in size, and the J2 become preinfective J2 (Fig. 2C) just before molting to the IJ, which retain the J2 cuticle as a sheath. J2 dissected from an infected cricket in 0.1 ml water and left in the mixture of body fluids and water, all become IJ in 24–36 hours.

Third-stage noninfective juvenile (J3) of the first generation: Immediately after an IJ enters the hemocoel of a mole cricket, the walls of the stoma thicken and the lumen opens (Fig. 2F). Then the mouth opens revealing a funnel-shaped stoma (Fig. 2G). The anterior part of the esophagus, which was thin in the IJ (Fig. 3L), now thickens gradually. The bacterial chamber in the anterior region of the intestine enlarges and the bacteria move posteriorly until they are released through the anus into the hemocoel of the host. After IJ enter a host, it takes less than 24 hours for them to become feeding J3. During this time, the walls of the stoma thicken and two small refractive dots (rhabdions) are observed on each side of the stoma (Fig. 2G). These dots become darker and the anterior one enlarges. The stoma and esophagus become typical of the J3 of the genus *Steinernema* (Fig. 2H) about 36 hours after penetration, at which time the J3 molt to the J4. Body length ranged from 651 μm to 958 μm and the width from 30 μm to 48 μm (n = 10).

Third-stage noninfective juvenile (J3) of the second generation: The J3 of the second generation can be recognized by the color of the body, which, depending on food supply, may be yellow-brown to dark. The body size is variable, but it is larger than the J2 of the second generation. The cheilorhabdions are thick (Fig. 2E). The intestinal lumen is prominent. The tail is shorter than that of the J2 and tapers abruptly immediately posterior to the anus. Some J3 had a small postanal swelling (Fig. 3F), and those became females; those without a postanal swelling (Fig. 3G) became males. The J3 molt to the J4 in about 24 hours. The body length ranged from 723 μm to 952 μm and the width from 42 μm to 60 μm (n = 10).

Third-stage infective juvenile (IJ): The body is thin with an average length of 572 ± 27 μm and a width of 24 ± 4 μm (n = 20). The cuticle of the J2 is retained as a sheath, but it may or may not be present because it is lost easily. The lip region is continuous, the oral aperture and stoma are closed (Fig. 2D), and the esophagus is reduced in size (Fig. 3L). The tail is attenuate, tapering gradually dorsally and abruptly ventrally. When specimens are relaxed, the tail usually curves ventrally at an angle of 110 degrees with the body. A full description of the IJ and the first- and second-generation adult males and females is contained in Nguyen and Smart (8).

Fourth-stage juvenile (J4) male: The J4 is larger, the body is darker, and the tail is shorter and tapers more abruptly than that of the J3. The gonad is almost completely developed, and the stoma and esophagus are similar to those of the adult. The spicules and gubernaculum begin to develop with development occurring distally to proximally. The tail curves ventrally, tapering abruptly immediately posterior to the anus. This stage usually lasts 12–24 hours. The adult stage within the fourth-stage cuticle can be recognized by the fully formed spicules, gubernaculum, and gonad, and by the mucron on the tail of the adult. The first- and second-generation J4 males are similar, except that the latter is smaller than the former. In the same host, the J4 male molts to the adult before the female does.

Fourth-stage juvenile (J4) female: The stoma and esophagus are similar to those of the adult (Fig. 2I). The vulva and vagina begin to develop and the ovaries become prominent. The elliptically shaped struc-

ture in the excretory system (8) is present, although not as prominently as in the adult. This structure was not prominent in the J4 of the second generation. The J4 stage lasted 12–24 hours before molting to the adult stage. The body length of the first-generation J4 females ranged from 1,000 μm to 2,468 μm and the width from 72 μm to 108 μm (n = 10). The length of the second-generation J4 females ranged from 897 μm to 1,439 μm and the width from 54 μm to 90 μm (n = 10).

Adult males (first generation): The body is 1,728 ± 358 μm long and 156 ± 49 μm wide (n = 10), yellowish-brown with the posterior end curved ventrally and terminated by a mucron. The gonad is monorchic, reflexed; the paired spicules are dark brown and the blade tapers gradually to a tip. The gubernaculum is boat-shaped with a thin anterior part. The cloacal area is raised and bears an anterior flap. There are 10 pairs and one single genital papillae.

Adult males (second generation): These males are similar to those of the first generation except that they are shorter (1,147 μm vs. 1,728 μm) and about half as wide (73 μm vs. 156 μm). Also, the spicules have an elongate head, in contrast to an angular head in the first generation (Fig. 4).

Adult females (first generation): The body is 4,162 ± 540 μm long and 179 ± 13 μm wide (n = 10), dark brown or black, and generally contains many eggs. The cheilorhabdions are heavily thickened and prominent (Fig. 3A). The esophagus is typical of the family. The excretory duct forms a prominent loop at the base of the esophagus. The gonads are didelphic, amphidelphic, reflexed. The vulva, near midbody, is a transverse slit bearing a prominent double-flapped epiptygma. The tail is short, with a large postanal swelling, usually mucronate (Fig. 3I).

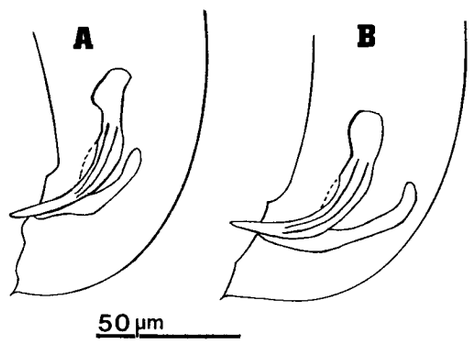

FIG. 4. Spicules of *Steinernema scapterisci*. A) Spicule of first-generation male. B) Spicule of second-generation male.

Adult females (second generation): These females are similar to those of the first generation except they are smaller (2,209 ± 223 μm long and 123 ± 14 μm wide). The valve in the basal bulb of the esophagus is more prominent and the loop in the excretory system is less prominent than in first-generation females. The tail tapers to a point bearing a mucron (Fig. 3H).

Influence of temperature on the life cycle: At 10 C the IJ never reached the adult stage (Table 1). A few began to develop to the fourth stage but had poorly developed, shortened, plump bodies, and all died within 5 days after exposure to the hosts.

At 15 C the IJ developed in the thoracic cavity into males and females of the first generation 10 days after exposure to the host. The J1 first appeared after 15 days. Most, but not all of these J1 moved to the abdominal cavity and embedded themselves in the fat tissue lining the abdominal wall. The J1 moved very slowly. By the 18th day after exposure, the size of the J1 had not increased, and they become immobile and died.

At 20 C the IJ developed to first-generation males and females in 7 days, but many of them died. Those that remained alive were not very active. Second-generation adults appeared 8 days after exposure to hosts. Second-generation IJ appeared 10 days after exposure, with many appearing by day 12.

At 24 C the IJ developed to first-generation adults in 3 days after exposure to the hosts. Most of these adults were in the anterior part of the cricket cadaver. After 4 days, most of the first-generation adults had produced eggs, died, and decayed, but a few dead females containing

TABLE 1. Influence of temperature on the life cycle of *Steinernema scapterisci*.

Temp. (C)	No. of days to first appearance			
	1GA†	2GA‡	Short cycle	Long cycle
10	NC§	ND	ND	ND
15	10	NC	ND	ND
20	7	8	10	12
24	3	7	7	9
30	2	5	6	8
33	2	5	6	8
35	NC	ND	ND	ND
37	ND	ND	ND	ND

† First-generation adult.
‡ Second-generation adult.
§ NC = not complete; ND = not developed.

J1 remained. These J1 emerged from the body of the females and migrated to all parts of the cricket. After 7 days, preinfective J2, IJ (short cycle), and second-generation adults were present both inside and outside the cricket cadavers. By day 8, preinfective J2 and IJ were abundant. By day 9, eggs produced by the second-generation females developed to J1, to preinfective J2, and then to IJ. In the preinfective J2, the esophagus and stoma were not well-developed and a chamber containing bacteria was forming (Fig. 3K). The J2 molted to the IJ and retained the J2 cuticle as a sheath. At day 10, IJ populations were abundant. Thus, the short cycle took 7 days to complete and the long cycle 9 days at 24 C.

At 30 C the IJ developed to first-generation adults in 2 days after exposure to hosts. Some eggs produced by these females developed into IJ (short cycle) in 6 days and others into second-generation adults in 5 days. IJ from the second-generation females first appeared in 8 days, and large populations were present by day 10.

At 33 C IJ developed into adult males in 1 day and females in 2 days after exposure to hosts. At this time, some females contained J1 in their bodies, indicating that the females became adults, mated, and produced eggs in less than 2 days. IJ (short cycle) and second-generation adults appeared after 6 days. Some of these females contained J1. The eggs produced by the second-generation females became IJ in 8–9 days. About 5% of the house crickets contained a large number of dead adult nematodes.

At 35 C no live nematodes were observed in the house crickets 2 days after exposure to IJ. One to five dead adult males, but no females or juveniles, were found in 5 of the 100 crickets dissected.

At 37 C no live or dead nematodes of any stage were found in the 100 house crickets dissected.

Influence of temperature on sex ratio of first-generation adults: At 15 C the first-generation female/male ratio was 1.2:1 (139/118) (Table 2). The nematodes did not develop beyond this stage. At 24 C the first-generation female/male ratio was 1.5:1 (62/42). At 30 C the first-generation female/male ratio was 0.9:1 (33/37). Thus, when the temperature increased from 15 to 24 C, the percentage of females increased ($P < 0.01$); but when the temperature increased from 24 to 30 C, the percentage of females decreased ($P < 0.01$). Observations showed that one male can mate with more than one female. Consequently, the greater number of females at 24 C may increase the production of IJ, but the lower number of females at 30 C may reduce the production of IJ. Linear regression analysis of the above data shows a negative relationship between the percentage of females (Y) and the total number of nematodes (X) produced in a house cricket at 24 C (Fig. 5). When the total number of adult females and males in a house cricket was ≤ 83 (in 8 of 12 crickets),

TABLE 2. Number and percentage† (with range in parentheses) of first-generation females and males of *Steinernema scapterisci* that developed at 15 C, 24 C, and 30 C in each house cricket.

	No. ♀	% ♀	No. ♂	% ♂	Total
15 C	139 ± 57 a	54 ± 6 b	118 ± 41 a	46 ± 6 a	257 ± 94 a
	(61–231)	(40–60)	(47–202)	(40–60)	(108–406)
24 C	62 ± 34 b	64 ± 8 a	42 ± 36 b	36 ± 7 b	104 ± 69 b
	(19–125)	(62–76)	(10–107)	(24–48)	(29–232)
30 C	33 ± 20 b	47 ± 10 b	37 ± 30 b	53 ± 10 a	70 ± 48 b
	(6–65)	(27–72)	(5–102)	(28–73)	(11–143)

† Means of 10 replicates at 15 C and 12 replicates at 24 and 30 C.
Numbers with the same letters in the same column are not significantly different ($P < 0.01$) according to Duncan's multiple-range test.

the average female/male ratio was >2:1; in some individual crickets, the female/male ratio was >3:1. When the total number was greater than 83, the average female/male ratio was about 1:1. The linear relationship between the percentage of females and the total number of nematodes in a house cricket at 15 C to 30 C was not significant.

DISCUSSION

The life cycle of *S. scapterisci* is similar to that described for other species of *Steinernema,* having both the short cycle (one adult generation) and the long or normal cycle (two adult generations).

The life cycle is temperature-dependent and was not completed at the lower temperatures of 10 and 15 C or at the higher temperatures of 35 and 37 C. The optimum temperature is about 24 C, but because the cycle is completed up to and including 33 C, the likelihood of the nematode surviving in southern climates is enhanced. However, because the cycle was not completed at 15 C or lower, the nematode may not survive in colder climates.

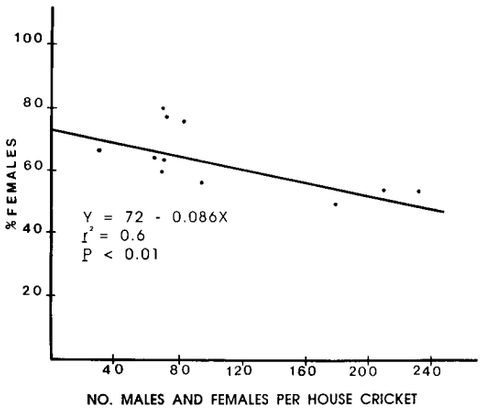

FIG. 5. The relationship between the percentage of females and the total number of nematodes in each house cricket.

There were some similarities in the effects of temperature on the life cycle of *S. scapterisci* and *S. carpocapsae,* but *S. scapterisci* was more tolerant of higher temperatures and less tolerant of lower temperatures than was *S. carpocapsae.* Kaya (6) reported that *S. carpocapsae* strain DD-136 did not reproduce at 10, 15, or 30 C and above. At 15 C, he found all stages of the nematode by dissecting the infected *Galleria* larvae, but no IJ emerged up to 21 days. It reproduced well at 20 and 25 C, with 25 C the optimum temperature. Danilov (2) reported that the life cycle of *S. carpocapsae* strain Agriotos was completed at temperatures from 15 to 28 C, but that the cycle took 60 days to complete at 15 C. The optimum temperature was 25 C. Hackett and Poinar (5) reported that when adult honeybees kept at 34 C were exposed to IJ of *S. carpocapsae* strain Agriotos, adult nematodes developed. However, if the infected bees were dissected more than 3 days after death, breeding populations of the nematode were present. They did not say whether the bees were kept at 34 C after they died.

The greatest average number of first-generation females and males, 257, was produced in house crickets at 15 C. This number was approximately two and four times as great as the numbers produced at 24 and 30 C, respectively. This was sur-

prising because the life cycle was not completed at 15 C. One reason for a greater number of females and males at 15 C may be that the nematodes had been maintained at 6–10 C and the crickets at 22–24 C. A temperature of 15 C would slow the activity of the crickets but would increase the activity of the nematodes. Thus, a greater number of IJ may have entered the house crickets. However, this was not a suitable temperature for subsequent development, and the nematodes died. This information may be useful for producing greater populations of IJ by in vivo culture. If IJ stored at 6–10 C and host crickets kept at ambient temperatures were placed in an inoculation chamber at 15 C until the house crickets died and then transferred to 24 C for development of the nematode, larger numbers of IJ should be produced.

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