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Host-Parasite Biology of *Thripinema fuscum* (Tylenchida: Allantonematidae) and *Frankliniella fusca* (Thysanoptera: Thripidae)[1]

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Abstract: *Thripinema fuscum* is a natural enemy of *Frankliniella fusca* in peanut. Laboratory experiments were conducted to determine the reproductive biology of *T. fuscum* as affected by gender and stage of development of the host and to determine the effects of parasitism on host longevity, fecundity, and mortality. The adult females of *F. fusca* were the most readily parasitized ($P < 0.001$) in the laboratory experiments followed by the second instars, the first instars, and the adult males. One generation of *T. fuscum* developed within the parasitized larvae and adults, with the males and females emerging only during the adult stage of the host. Parasitism did not cause mortality of the host. Parasitism affected male longevity ($P < 0.001$) but not female longevity. The adult female thrips that were parasitized as first or second instars did not lay eggs, and the adult females stopped laying eggs within 3 days of being parasitized. The female-to-male sex ratio of *T. fuscum* emerging from parasitized male and female *F. fusca* was 22 and 18 to 1, respectively. More *T. fuscum* emerged from female hosts than from male hosts ($P < 0.001$). More emerged from hosts parasitized as larvae compared with hosts parasitized as adults ($P < 0.05$). The intrinsic capacity of increase of *T. fuscum* ranged between 0.29 and 0.37 when parasitizing the adult males and females and between 0.18 and 0.21 when parasitizing the larval males and females. Percent parasitism of *F. fusca* was estimated in peanut fields. The flowers were the primary site for aggregation of the adults of *F. fusca* and for the free-living females of *T. fuscum* to parasitize new hosts. As under laboratory conditions, field parasitism of adult males was less than parasitism of adult females in 2001 and 2002 ($P < 0.01$ and 0.001, respectively). Our study indicates that *T. fuscum* is a potential biological control agent capable of suppressing *F. fusca* populations in peanut.

Key words: allantonematidae, *Arachis hypogaea,* biological control, entomopathogenic nematode, *Frankliniella fusca,* host-parasite biology, nematode, population dynamics, Thripidae, *Thripinema fuscum* thrips.

The most common thrips species inhabiting and reproducing in peanut (*Arachis hypogaea*) in Florida is *Frankliniella fusca*. The larvae and adults inhabit the terminal buds and flowers, and adults are found on the seedlings as soon as plants emerge (Funderburk et al., 2002a). The adults are either macropterous (wings developed) or brachypterous (wings vestigial).

Relatively few natural enemies of thrips have been identified. Loomans et al. (1997) proposed that the large size of potential natural enemies restricts their entry into the preferred microhabitat of thrips. Insect parasitic nematodes, on the other hand, accumulate in the same microhabitat as many thrips species. An entomogenous nematode (Tylenchida: Allantonematidae) was found parasitizing *F. fusca* in Florida and described by Tipping et al. (1998) as *Thripinema fuscum*. Infective females enter *F. fusca* by penetrating through the intersegmental membranes, including those affiliated with the coxal cavities. According to early work by Lysaght (1936) on *Thripinema,* once a female enters the body cavity of the host, it molts and the cuticle deteriorates, leaving only the stylet, a shrunken part of the esophagus leading into a small bulb-like structure, a mass of cells positioned centrally, and an oval gonad. Eventually the gonad elongates and folds upon itself As these changes occur, the nematode swells to a sac-like organism that appears immobile. The oviparous female releases oval-shaped eggs into the host haemocoel. Immature nematodes go through three juvenile stages before developing into infective adults.

Sharga (1932) reported that *Thripinema aptini* (Sharga) juveniles in the abdominal haemocoel of a thrips host use their stylet to bore from the midgut or oviduct to the pyriform rectum. The juveniles remain in the rectum for a period of time before exiting through the anus, usually with the insect's frass. The stylet is either reduced or missing in the males of *Thripinema* species (Tipping et al., 1998). Sharga (1932) reported that males were never found in the rectum of the host nor were they observed exiting through the anus. Only females parasitize hosts, and more than one parasitic female can enter a single thrips (Lysaght, 1937; Sharga, 1932). Lysaght (1937) reported that fertilization may occur in the host before the juveniles exit via the anus. Mating of *Thripinema* spp. was believed by Nickle and Wood (1964), Reddy et al. (1982), Chizhov et al. (1995), Tipping et al. (1998), and Siddiqi (2000) to occur outside the host on plant structures.

All known species in the genus *Thripinema* cause sterilization of the host, although the physiological mechanisms are not well understood (Loomans et al., 1997). Lysaght (1937) presumed that parasites cause sterility either by depriving the thrips of protein required for normal egg development or by secreting a toxin that damages the reproductive organs. An alternative hypothesis is that the stretch receptors in the thrips ab-

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domen that normally regulate oogenesis may respond to the increasing number of nematodes by signaling the ovaries to halt oogenesis as if maximum egg capacity had been attained (Green and Parella, 1995). Regardless, parasitization induces noticeable changes in the shape of the oviduct, vagina, and receptaculum seminis of female thrips (Loomans et al., 1997).

We conducted studies of host/parasite biology of *F. fusca* and *T. fuscum.* Laboratory experiments were conducted to determine the reproductive biology of *T. fuscum* as affected by gender and stage of development of the host and to determine the effects of parasitism on host longevity, fecundity, and mortality. Peanut fields were sampled to determine percent parasitism of different wing forms, genders, and stages of *F. fusca* and contrasted against whether they were collected from the flowers or the terminal buds of peanut.

Materials and Methods

Thrips colonies: 'Florunner' peanuts were planted in 14-cm-diam. pots with Fafard Professional Formula 3B Mix soil (Agawam, MA) and maintained at 25 °C to 30 °C in a greenhouse. Tetrafoliolate leaves used in the laboratory experiments came from plants that were 2 to 12 weeks old. *Frankliniella fusca* were collected in Alachua County, Florida, from ornamental peanuts (*Arachis pintoi* Krap. & Greg.). Thrips were tested for parasitism by placing them in 1.5-ml Eppendorf microcentrifuge tubes with a 1-cm-diam. peanut leaf disc and incubated at 23 °C with a 14-hour light period. The tubes were rinsed after 24 hours with 100 µl of water, and the number of male and female *T. fuscum* were determined at 100× magnification. Healthy thrips colonies were maintained in 15-cm polypropylene containers with a 5-cm diam. ventilation hole covered with fine mesh. The polypropylene containers were stored in sealed plastic crispers lined with moist paper towel and maintained at 27 °C with a 14-hour light period. Four to eight fresh tetrafolioliate leaves were deposited into the containers every other day, and old peanut tetrafoliolate leaves were saved in polypropylene containers for the subsequent harvest of larvae. The colonies were periodically tested for accidental parasitism by *T. fuscum. Frankliniella fusca* parasitized by *T. fuscum* were obtained from peanut growing in Jackson County, Florida. Parasitism was maintained by holding parasitized thrips in a 1.5-ml Eppendorf microcentrifuge tube with a 1-cm-diam. peanut leaf disc and adding larvae as needed. Larvae were removed after 72 hours and housed in a separate polypropene container with peanut tetrafoliolate leaves and maintained at 23 °C and a 14-hour light period.

Influence of parasitism on host fecundity, longevity, and mortality: Fecundity, adult longevity, and mortality of nonparasitized and parasitized *F. fusca* were determined in the laboratory at constant 23 °C and 14-hour light period. Cohorts of 1-day-old first instars, 1-day-old second instars, 1-day-old adult females, 1-day-old adult males, 3-day-old females, and 6-day-old females were enclosed in 1.5-ml Eppendorf microcentrifuge tubes with two parasitized individuals and a leaf disc dusted with peanut pollen. After 24 hours, the thrips were placed individually in a vial with a fresh leaf disc dusted with peanut pollen. The thrips were transferred to a new vial every 24 hours, and the original vials were rinsed with 100 µl of water and centrifuged at 500 rpm for 3 min. After siphoning 90 µl from the vial, the remainder was examined to determine the number of nematodes under 100× magnification. Nonparasitized thrips of each treatment served as healthy controls. The number of male and female of *T. fuscum* excreted each day were determined. Adult longevity of *F. fusca* was recorded as the number of days from adult emergence to death. Thrips were dissected after death to ensure that parasitized thrips were not accidentally recorded as healthy. Mortality was recorded as the number surviving less than 4 days. The effect of parasitism on the mortality of male and female larvae and adults of *F. fusca* was determined using logistic regression with a logit link and binomial distribution (PROC GENMOD, SAS Institute, Cary, NC) (Stokes et al., 1991). A subsequent likelihood ratio test for type 3 analysis was used to evaluate significance of the parasitism effect at the 0.05 level. The effects of parasitism on the longevity of the females and males and on the fecundity of the females were made using individual t-tests for each age and stage (SAS PROC TTEST). The total number of male and female *T. fuscum* emerging from each stage, age, and gender of the host were compared using the SAS general linear model. Only data for hosts living greater than 4 days were included in this analysis. The intrinsic capacity of increase (r_c) of *T. fuscum* was estimated for each stage, age, and gender of the host by

$$\ln (R_0)/T_c,$$

where R_0 is the net reproductive rate (females produced per female per generation) and T_c is the cohort generation time (from time of parasitization until death of the host). The r_c values allow for comparison of how biotic potential varies when *T. fuscum* parasitizes different *F. fusca* hosts (Price, 1975).

Susceptibility of adults and larvae to parasitism: Laboratory tests were used to determine the susceptibility of first instars, second instars, adult males, and adult females of *F. fusca* to parasitism by *T. fuscum.* Twenty were placed as single-stage cohorts in individual 1.5-ml Eppendorf microcentrifuge tubes with two parasitized female thrips and a 1-cm peanut leaf disc. The vials were maintained at 23 °C and a 14-hour light period. After 72 hours, each thrips was dissected and the number of *T. fuscum* was recorded. The experiment was replicated three times. Differences between percentage parasitism among life stages were compared using logistic regres-

sion with a logit link and a binomial distribution and a subsequent likelihood ratio test for a type 3 analysis at the 0.05 level of probability. Comparisons among life stage in the intensity of parasitization were analyzed using the general linear model.

In-vivo development of T. fuscum: Twenty-five second instars were exposed to two parasitized female *F. fusca* in a 1.5-ml Eppendorf microcentrifuge tube containing a 1-cm peanut leaf disc. The vials were maintained at 23 °C and a 14-hour light period. After 24 hours, the larvae were placed in individual Eppendorf tubes with a fresh peanut leaf disc. Two parasitized thrips were dissected every day, and the developmental stages of *T. fuscum* in the haemocoel were recorded.

Influence of wingform, gender, and stage on parasitism in peanut fields: Peanut fields were established in 2001 and 2002 at the North Florida Research and Education Center in Jackson County, Florida. Flowers and terminal buds were sampled at each of three locations on 10 August 2001 and 15 August 2002 to compare parasitism among first instars, second instars, adult males, and adult females. The flowers and terminal buds were gently swirled in detergent solution to remove the thrips. Thrips were collected by sequentially straining the solutions through 46 × 92-cm Cheesecloth Wipes and 9-cm-diam. Fisherbrand grade P8 Filter Paper (Fisher Scientific Co., Pittsburgh, PA). Filter papers were examined under a stereomicroscope at 40× magnification. At each location, attempts were made to collect 25 adult males of each wing form, 25 adult females of each wing form, 25 first instars, and 25 second instars from both the flowers and the terminal buds. Individuals were dissected to determine the presence of *T. fuscum*. A logistic regression with a logit link and a binomial distribution was used to determine the effects of location in the field, location on the plant, gender, and wing form on parasitization of the adult females and males. Only data for the adults were analyzed because the inability to determine the wing form and gender of larvae would have caused interdependencies in the analyses. Parameters in which the main effect or any of its interactions were significant ($P < 0.05$) in the subsequent likelihood ratio tests (type 3) were included according to the hierarchal principle in a separate logistic regression model. Additional samples were taken on 10 August 2001 and 15 August 2002 to estimate the number of larvae and adult *F. fusca* per peanut flower and terminal. Ten flowers and terminals from each of the three locations in each field were placed in vials containing 70% alcohol and returned to the laboratory where, they were examined under 40× magnification.

Results

Influence of parasitism on host mortality, longevity, and fecundity: Parasitism of the males and females of *F. fusca* by *T. fuscum* did not affect mortality that were initially parasitized as larvae or adults ($X^2 = 0.1$, df = 1, $P > 0.0.5$). Parasitism of the adult males by *T. fuscum* reduced mean longevity ± SEM from 9.2 ± 0.6 to 7.6 ± 0.3 days ($t = 2.5$, df = 48, $P < 0.001$). Adult longevity was not reduced when the males were parasitized as first or second instar ($t = -0.3$ and -0.4, respectively; df = 24 and 25, respectively; $P > 0.05$). Mean adult longevity ± SEM of the nonparasitized females in the laboratory experiments was 13.3 ± 0.9 days. Parasitism of the 1-day-old, 3-day-old, and 6-day old females did not reduce longevity ($t = 0.3$, 0.1, and 0.0, respectively; df = 48; $P > 0.05$).

Nonparasitized females of *F. fusca* laid a mean ± SEM of 1.67 ± 0.21 eggs per day for a mean total of 23.0 ± 1.6 eggs per female (Fig. 1). Parasitism of the first instars, second instars, 1-day-old adults, 3-day-old adults, and 6-day-old adults reduced fecundity ($t = 17.7$, 14.1, 11.5, 6.5, and 8.3, respectively; df = 48; $P < 0.001$). Females parasitized as first or second instar did not lay eggs. Females parasitized at 1, 3, and 6 days of adult age laid eggs for a maximum of 3 days after parasitization. The mean number + SEM of total eggs laid after parasitization was 1.5 ± 0.4, 3.1 ± 0.5, and 2.9 ± 0.5 for the females that were parasitized at 1, 3, and 6 days of adult age, respectively.

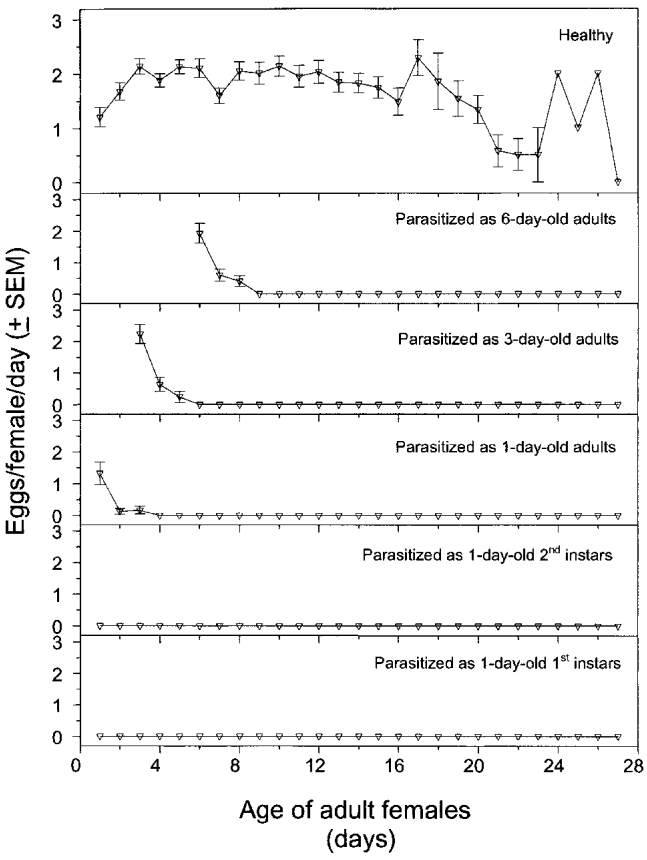

Fig. 1. The mean number of eggs laid per female per day (±SEM) for healthy *Frankliniella fusca* and those parasitized by *Thripinema fuscum* as 1-day-old first instars, 1-day-old second instars, 1-day-old adults, 3-day-old adults, and 6-day-old adults under laboratory conditions of 23 °C and 14-hour light period.

The numbers of male *T. fuscum* emerging from parasitized *F. fusca* were low when compared with the numbers of emerging females. The mean number ± SEM of male nematodes emerging per day from the female *F. fusca* parasitized as first instars, second instars, 1-day-old adults, 3-day-old adults, and 6-day-old adults was 0.8 + 0.1, 0.4 ± 0.1, 0.7 ± 0.1, 1.2 ± 0.2, and 1.6 ± 0.5, respectively (Fig. 2). The mean number ± SEM of male nematodes emerging per day from male *F. fusca* parasitized as first instars, second instars, and 1-day-old adults was 0.3 ± 0.1, 1.1 ± 0.2, and 0.1 ± 0.1. respectively (Fig. 3). The mean number ± SEM of female nematodes emerging per day from female *F. fusca* parasitized as first instars, second instars, 1-day-old adults, 3-day-old adults, and 6-day-old adults was 13.9 ± 1.0, 14.8 ± 1.0, 15.3 ± 0.7, 10.7 ± 0.9, and 7.3 ± 1.4, respectively (Fig. 2). The mean number ± SEM of female nematodes emerging per day from male *F. fusca* parasitized as first instars, second instars, and 1-day-old adults was 10.6 ± 0.7, 12.4 ± 0.8, and 11.2 ± 1.0, respectively (Fig. 3). The ratio of female to male *T. fuscum* emerging from male and female hosts was 22 and 18 to 1, respectively.

The mean total number ± SEM of male and female *T. fuscum* emerging from parasitized male and female *F. fusca* of different larval and adult ages is shown in Table 1. The mean number of females emerging was affected

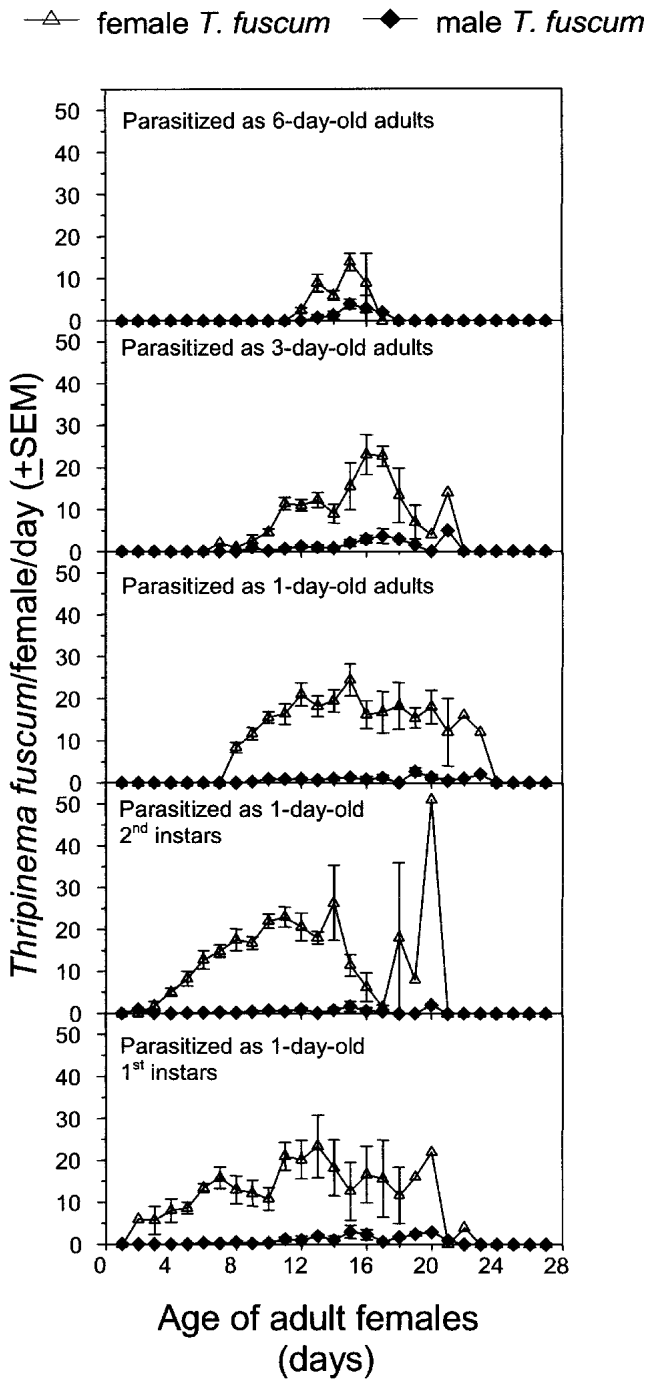

FIG. 2. The mean number of male and female *Thripinema fuscum* excreted per female *Frankliniella fusca* per day (±SEM) for those parasitized as 1-day-old first instars, 1-day-old second instars, 1-day-old adults, 3-day-old adults, and 6-day-old adults under laboratory conditions of 23 °C and 14-hour light period.

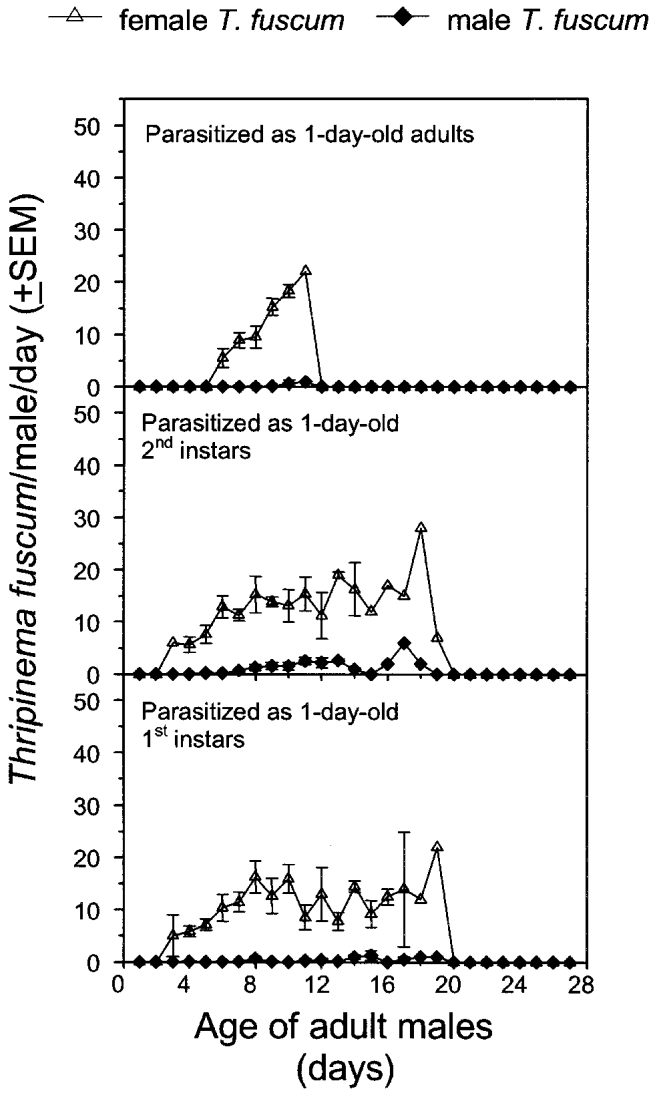

FIG. 3. The mean number of male and female *Thripinema fuscum* excreted per male *Frankliniella fusca* per day (±SEM) for those parasitized as 1-day-old first instars, 1-day-old second instars, and 1-day-old adults under laboratory conditions of 23 °C and 14-hour light period.

TABLE 1. The mean number (±SEM) of male and female *Thripinema fuscum* emerging per *Frankliniella fusca* surviving at least 4 days post-parasitization and the intrinsic capacity of increase (r_c) values of *Thripinema fuscum* as influenced by the gender of the host and the age when parasitized.

Gender of host	Age of host	Mean number ± SEM per host		r_c of *Thripinema fuscum*
		Male	Female	
Female	1-day-old 1st instars	8.4 ± 2.4 a	145.4 ± 39.1 a	0.21
	1-day-old 2nd instars	3.7 ± 1.1 bc	133.5 ± 27.2 a	0.21
	1-day-old adults	4.8 ± 0.9 ab	103.9 ± 15.1 a	0.35
	3-day-old adults	4.6 ± 1.4 b	41.0 ± 10.6 b	0.37
	6-day-old adults	2.8 ± 2.0 bc	18.0 ± 6.2 b	0.29
Male	1-day-old 1st instars	1.8 ± 0.2 c	74.6 ± 19.0ab	0.18
	1-day-old 2nd instars	7.8 ± 2.0 ab	88.9 ± 19.6 a	0.20
	1-day-old adults	0.2 ± 0.1 c	23.5 ± 4.7 b	0.34

Means in a column followed by the same letter are not significantly different according to a general linear model (df = 7, 142) and subsequent least squares means ($P < 0.05$).

by the gender and stage of the host ($F = 12.0$; df = 7, 142; $P < 0.0001$). The greatest number of female nematodes emerged from the female *F. fusca* parasitized as larvae and 1-day-old adults. An intermediate number of female nematodes emerged from male *F. fusca* parasitized as larvae. The least number of female nematodes emerged from the male *F. fusca* parasitized as 1-day-old adults and the female *F. fusca* parasitized as 3-day-old and 6-day-old adults. The mean number of male nematodes emerging also was affected by the gender and the age of the host ($F = 7.1$; df = 7, 142; $P < 0.0001$). *Thripinema fuscum* had the greatest capacity of increase when parasitizing adult male and female *F. fusca* and the least when parasitizing larvae (Table 1).

Susceptibility of adults and larvae to parasitism: *Thripinema fuscum* parasitized all the life stages of *F. fusca* tested (Table 2). There were differences among parasitism of first instars, second instars, and adult males and females ($X^2 = 22.8$; df = 3; $P < 0.001$). Adult males were the least parasitized and adult females the most parasitized. During the infection process, larvae and adults of *F. fusca* were usually parasitized by one parasitic female of *T. fuscum* (Table 2), although as many as six parasitic females were detected in one adult female. There were no differences in the mean number of *T. fuscum* parasitizing the larvae and the adults *F. fusca* ($F = 1.0$; df = 3, 110; $P > 0.05$).

In-vivo development: Adult male and female *T. fuscum* began emerging from *F. fusca* adults 9 days following parasitization of the second instars (Table 3). The female *T. fuscum* began swelling 2 days post-parasitization. Parasitic females developed the mature oval shape 4 days post-parasitization. At this time, the first nematode eggs were observed in the host haemocoel. The parasitic female of *T. fuscum* continued to lay eggs until the death of either the host or the parasite. Juvenile stages of *T. fuscum* were initially observed within the host 6 days post-parasitization.

Influence of wing form, gender, and stage on parasitism in peanut fields: Mean percent parasitism ± SEM of first instars, second instars, adult males, and adult females of *F. fusca* in the terminal buds and flowers of peanut on 10 August 2001 and 15 August 2002 are shown in Table 4. The mean number + SEM of first instars, second instars, adult males, and adult females per peanut terminal and flower also are given in Table 4. The adults were aggregated in the flowers, and the larvae were aggregated in the terminal buds. The percent brachyptery of females and males of *F. fusca* was 29.6% and 34.0%, respectively, in 2001 and 5.6% and 21.2%, respectively, in 2002. The ratio of females to males was 5.1 and 2.0 to 1 in 2001 and 2002, respectively.

The initial logistic regression analyses for 10 August 2001 and 15 August 2002 evaluated the main and interactive effects of location in the field, location on the

TABLE 2. Mean % parasitism and mean number of parasitic females of *Thripinema fuscum* per parasitized *Frankliniella fusca* in a laboratory choice experiment ($n = 3$ replicates of 20 individuals per stage of host).

Stage of host	% Parasitized[a]	Mean number per parasitized host[b] (maximum number in parentheses)
First instars	45 b	1.2 (2)
Second instars	53 ab	1.3 (3)
Adult females	67 a	1.4 (6)
Adult males	25 c	1.1 (2)

[a] Percentages within the column followed by the same letter are not significantly different according a logistic regression and subsequent likelihood ratio tests ($P < 0.05$).

[b] Means within the column are not significantly different according to a general linear model ($P > 0.05$).

TABLE 3. The developmental stages of *Thripinema fuscum* observed daily for 9 days post-parasitization of *Frankliniella fusca.*

Days after parasitization	Developmental stage of host	Developmental stages of *Thripinema fuscum* observed
1	1st Instar	Parasitic female
2	2nd Instar	Parasitic female noticeably swollen
3	Prepupa	Parasitic female much swollen
4	Pupa	Mature parasitic females, eggs
5	Pupa	Mature parasitic females, eggs
6	Adult	Mature parasitic females, eggs, juveniles 2
7	Adult	Mature parasitic females, eggs, juveniles 2 and 3
8	Adult	Mature parasitic females, eggs, juveniles 2 and 3, adult males and females
9	Adult	Mature parasitic females, eggs, juveniles 2 and 3; adult males and females; emergence from host

TABLE 4. The mean density and percent parasitism (±SEM) of first instars, second instars, adult females, and adult males of *Frankliniella fusca* in peanut terminals and flowers in fields sampled on 10 August 2001 and 15 August 2002.

	10 August 2001				15 August 2002			
	Peanut terminals		Peanut flowers		Peanut terminals		Peanut flowers	
	Mean no. (± SEM)	% Parasitism (± SEM)	Mean no. (± SEM)	% Parasitism (± SEM)	Mean no. (± SEM)	% Parasitism (± SEM)	Mean no. (± SEM)	% Parasitism (± SEM)
1st Instars	0.13 ± 0.1	24 ± 0.0	0 ± 0	—	0.98 ± 0.4	1 ± 1.0	0.05 ± 0.0	0 ± 0
2nd Instars	0.40 ± 0.2	33 ± 3.5	0.03 ± 0.0	0 ± 0	0.93 ± 0.3	4 ± 1.6	0.18 ± 0.1	0 ± 0
Females	0.22 ± 0.1	32 ± 2.9	0.96 ± 0.2	56 ± 4.2	0.21 ± 0.1	11 ± 3.7	3.31 ± 1.0	28 ± 2.5
Males	0 ± 0	—	0.23 ± 0.1	31 ± 0.7	0.08 ± 0.0	0 ± 0	1.67 ± 0.4	4 ± 2.2

plant, wing form, and gender on percent parasitism of the adults. The main effect of location in the field and the interactive effects including location in the field were not significant ($P > 0.05$) in either analysis. Location on the plant, wing form, and gender of the *F. fusca* adults influenced percent parasitism, and their main and interactive effects were retained in the subsequent logistic regression analyses. The parameter estimates for the effects of location on the plant, gender, wing form, location on the plant-gender, and gender-wing form in the logistic regression model for 10 August 2001 were 0.43, 0.13, –0.61, –1.37, and 0.39 (X^2 = 1.3, 2.5, 4.2, 9.0, and 0.9, respectively; df = 1; P = 0.26, 0.12, 0.04, 0.003, and 0.34, respectively). The parameter estimates for the effects of location on the plant, gender, wing form, location on the plant-gender, and gender-wing form in the logistic regression model for 15 August 2002 were –0.73, –2.1, 0.32, –0.47, and 0.88 (X^2 = 25.6, 6.3, 29.5, 4.6, 0.3, and 1.4, respectively; df = 1; P = 0.0001, 0.01, 0.03, 0.59, and 0.23, respectively). The probability of parasitization on 10 August 2001 and 15 August 2002 of adult *F. fusca* of both wing forms and genders in the terminal buds and flowers as determined using the logistic regression models is shown in Table 5. The females were more parasitized than the males each year, and the females inhabiting the flowers were more parasitized than the females in the terminal buds. The effect of wing form was not consistent over years. The brachypterous adults were more parasitized than the macropterous adults in 2001, but the opposite was true in 2002.

TABLE 5. The probability of parasitization by *Thripinema fuscum* of *Frankliniella fusca* of both wing forms and genders in the terminal buds and flowers of peanut fields sampled on 10 August 2001 and 15 August 2002 as determined by logistic regression analyses.

			Probability of parasitization (%)	
Gender of host	Wing form of host	Location of host on plant	10 August 2001	15 August 2002
Female	Macropterous	Flower	53.3	39.0
		Terminal bud	30.8	16.0
	Brachypterous	Flower	58.8	16.0
		Terminal bud	35.8	5.4
Male	Macropterous	Flower	24.9	4.6
		Terminal bud	33.7	2.3
	Brachypterous	Flower	38.0	3.4
		Terminal bud	48.4	1.7

DISCUSSION

The larvae and the adults of *F. fusca* were readily parasitized by *T. fuscum* under laboratory conditions, with the adult females the most susceptible to parasitism and the adult males the least susceptible. We did not evaluate the ability of *T. fuscum* to parasitize the prepupae and pupae of *F. fusca* because these stages occur in the soil where they are not likely to encounter an infective female of *T. fuscum.* Mason and Heinz (2002) reported that all stages of *F. occidentalis* tested were parasitized by *T. nicklewoodi* in laboratory experiments, with female pupae being the most-preferred and adult males the least-preferred stage.

Parasitism by *T. fuscum* did not affect survival or longevity of the females of *F. fusca.* Clearly, the host-parasite relationship of rapid and sustained multiplication without effect on the survival and longevity of female thrips provides advantages to *Thripinema* spp. Male longevity was reduced. Likewise, Lim et al. (2001) reported that the males of *F. occidentalis* parasitized by *T. nicklewoodi* died earlier than nonparasitized males and that the longevity of females was not affected by parasitism. Fecundity reduction is a common outcome of parasitism of invertebrate hosts (Hurd, 2001). Female *F. fusca,* whether parasitized as larvae or adults, laid few, if any, eggs. Similar effects on fecundity were reported for the other described species of *Thripinema* (Green and Parrella, 1995; Kolobova, 1926; Lim et al., 2001; Lysaght, 1937; Mason and Heinz, 2002; Nickle and Wood, 1964; Reddy et al., 1982; Sharga, 1932; Teulon et al., 1997; Tipping et al., 1998: Wilson and Cooley. 1972). Prior theories speculated that the juvenile parasites are responsible for stopping oogenesis and that host oogenesis is actively regulated by the female *T. fuscum.* For example, Green and Parella (1995) hypothesized that the juveniles stopped oogenesis by affecting the stretch receptors in the thrips abdomen that regulate oogenesis, and Hocking (1967) proposed that the

juveniles stopped oogenesis by directly feeding on the reproductive organs or associated tissues. Our results demonstrated that the juveniles were not responsible for blocking oogenesis. Juveniles of *T. fuscum* were not observed in the haemocoel of the host until 6 days after it was parasitized, whereas egg laying stopped within 3 days.

The aggregation of *F. fusca* larvae in the terminal buds explains, in part, why the larvae of *F. fusca* were less parasitized than the adult females under field conditions. Peanut flowers are the primary site for the free-living females of *T. fuscum,* and the terminal buds have negligible numbers of parasitic nematodes (Tipping et al., 1998). Previously, very little research has attempted to compare percent parasitism of larval vs. adult populations under field conditions. However, investigators have noted that the larvae of several thrips species are parasitized by *Thripinema* spp. Tipping et al. (1998) reported that the larvae of *F. fusca* in peanut fields were rarely parasitized by *T. fuscum.* Chizhov et al. (1995) reported finding the adults and larvae of *Thrips trehernei* Prisner and *T. physapus* L. parasitized by *Thripinema khrustalevi* (Chizov et al. 1995), and Funderburk et al. (2002b) found that the larvae and adults of *Frankliniella australis* (Morgan) were parasitized by *T. khrustalevi* isolate Chile.

Laboratory results showed *T. fuscum* is less likely to parasitize the adult males of *F. fusca.* Lysaght (1937) and Nickle and Wood (1964) reported that male thrips in field populations were not hosts for *T. aptini* and *T. nicklewoodi,* respectively. Funderburk et al. (2002b) reported that the males of *F. australis* in the flowers of *Cestrum parqui* (L'Herit.) were parasitized less by *T. khrusialevi* isolate Chile than females. The flowers of plant hosts are the mating sites for species of *Frankliniella* thrips (Crespi, 1993). There is a competitive breeding structure, and males guard the flowers where mating takes place (Terry and Gardner, 1990). The males more rapidly colonize the new flowers (Ramachandran et al., 2001). Inhabiting new flowers void of free-living nematodes also provides escape from parasitization.

It has been proposed that *F. fusca* overwinters as brachypterous females (Beckham et al., 1971; Chamberlin et al., 1993; Eddy and Livingstone 1931; Newsom et al., 1953). High levels of brachyptery in a species of thrips appear to be related to energy conservation and favorable habitats (Hood, 1940; Kamm, 1972; Koppa, 1970; Roff, 1994). In our studies, high levels of brachyptery in *F. fusca* occurred in the summer. Brachypterous individuals were affected differently than macropterous individuals in regard to parasitism by *T. fuscum.* We hypothesize that the greater movement of macropterous *F. fusca* between flowers early in the season likely increases contact with free-living *T. fuscum.* As parasitism increases in the field, the proportion of flowers inhabited by the free-living females of *T. fuscum* is greater, and the probability of parasitization of the less mobile brachypterous *F. fusca* (which spend more time in flowers than the more mobile macropterous females) is increased.

Female-biased sex ratios of 5.5 to 1 by Mason and Heinz (2002) and 6.0 to 1 by Lim et al. (2001) were reported for *T. nicklewoodi* parasitizing *F. occidentalis.* Sharga (1932) reported a sex ratio of 10.8 to 1 for *T. aptini.* The sex ratio of 19.2 to 1 for *T. fuscum* is even higher than these species. These female-biased sex ratios may suggest that species of *Thripinema* have a tendency toward parthenogenesis. Newly emerged female juveniles of *T. fuscum,* isolated from contact with any free-living males, successfully parasitize and reproduce inside a new host (personal observation). *Thripinema fuscum* may have no need to increase its genetic diversity when mating under environmentally stable conditions. However, unfavorable conditions may stimulate mating as a means for progeny to adapt to such conditions. If more than one parasitic female infects a host, it is possible that progeny of the two females will mate, but whether this occurs inside the host or outside remains unknown.

Lowry et al. (1992) found an intrinsic capacity of increase of 0.06 for *F. fusca* developing on peanut at 23 °C. The intrinsic capacity of increase for *T. fuscum* when parasitizing the adults of *T. fusca* at 23 °C was more than 5-fold greater. The larvae of *F. fusca* are suitable hosts for *T. fuscum.* However, adult females are preferred over the larvae. Parasitism of the adult females is advantageous to *T. fuscum,* as demonstrated by the high intrinsic capacity of increase values. Overall, our studies reveal that *T. fuscum* is well adapted to exploit populations of *F. fusca* in peanut. The intrinsic capacity of increase is several-fold greater than that of *F. fusca* when the larvae and adults of both sexes of the host are parasitized.

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