The Nematode Heterotylenchus autumnalis and Face Fly Musca autumnalis: A Field Study in Northern California

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Abstract: Heterotylenchus autumnalis was found in six northern California counties surveyed, and the incidence of nematode infection of face flies ranged from 4.7 to 43.8%. Intensive studies at a cattle ranch in Yuba County showed that population densities of the host and nematode infections were highest in flies from cow pats receiving full sun. Average host population density was 105.7 puparia per pat, and nematode infection averaged 38.6%. Pats in partial sun averaged 13.5 puparia and 13.1% nematode infection. No face fly was recovered from shaded pats. When data from pats first exposed during day or night were compared, no significant differences in host population density or nematode infection rates were apparent. Uninfected and superinfected flies were more frequent than predicted by a Poisson distribution.

Infected and uninfected female flies of all ages captured on white sticky traps appeared to feed with similar frequency upon a creamy substance which was probably acquired from cattle. However, older infected females fed less on blood and more upon dung than older uninfected females. Percent nematode infection and host population densities were highest in spring and early summer, declined to a midsummer low, and then increased slightly. Both dung-reared flies and captured females showed similar trends in abundance and infection rates. Regression analysis indicated that *H. autumnalis* may not be regulating face fly population density. *Key Words:* Biological control, host-parasite relationships, insect-nematode relationships, population dynamics.

Face fly, *Musca autumnalis* De Geer, is an introduced pest of cattle and other livestock in North America. Fourteen years after its accidental introduction, Stoffolano and Nickle (13) found it to be parasitized by an allantonematid nematode later described as *Heterotylenchus autumnalis* Nickle (6). Subsequently, infected flies have been reported from the eastern, central, and southern parts of the United States (2, 9, 11, 13, 15, 16).

Except for a brief free-living stage, the life cycle of the nematode occurs entirely within the host, alternating between gamogenetic and parthenogenetic stages (12). Infected female face flies undergo "mock ovipositions," depositing female and male nematodes ("nemapositing") in fresh cow dung. After mating, the male nematode dies, and the gamogenetic female penetrates the integument of a larval face fly developing within the dung. The nematode develops in the host's hemocoel and begins laying eggs shortly after the host emerges from its puparium. The eggs hatch into parthenogenetic females which deposit eggs that develop into male or female gamogenetic nematodes. These nematodes invade and distend the host's ovaries and are then nemaposited into dung. For infections to be maintained, both nemapositing and ovipositing face flies must visit the same fresh cow droppings (pats), and the gamogenetic nematodes must encounter susceptible fly larvae within the dung. Reproduction of parthenogenetic females is arrested in synchrony with the onset of reproductive diapause in newly emerged flies in the fall (10). As diapause development progresses, the flies leave the pastures and spend the winter in protective sites such as attics (1).

All studies of *H. autumnalis* and face fly have been conducted east of the Rocky Mountains. Consequently, a study was initiated to investigate the relationships between *H. autumnalis* and face fly in northern California. We report herein the following: 1) the occurrence of *H. autumnalis* in northern California; 2) the within-pasture distribution of the nematode and its host; 3) the frequency of nematodes within male and female hosts; 4) field evidence for the effects of *H. autumnalis* on its host; and 5) the seasonal dynamics of *H. autumnalis* in face fly.

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MATERIALS AND METHODS

The principal study site was a 112-ha beef cattle ranch adjacent to the University of California Sierra Foothill Range and Field Station in Yuba County, California. It was chosen because facilities were available nearby and no insecticides were used to control flies. Seventy-five Angus cows, calves, yearling steers, and heifers were present on the ranch throughout the study. The ranch was fenced into eight pastures: one uncleared pasture of 77 ha and seven cleared and improved pastures of 5 ha each. Two of the cleared pastures were alternately closed to animals and sprinkler-irrigated each week. A third cleared pasture was intermittently irrigated by ditch runoff. The remaining five pastures were not irrigated. Although seven of the eight pastures were open to grazing at all times, most of the cattle remained within or near the three irrigated pastures.

Six additional survey sites augmented the Yuba county site. Fly samples were collected at beef cattle ranches in Shasta, Mendocino, Lake, Placer, and Sonoma counties and at a dairy in Solano County. One collection was made in each county between June and September 1977.

Adult face flies were collected with a modified version of a white sticky trap developed by Pickens et al. (8). Each trap consisted of a 3-pound coffee can centered on a 3.5-cm-square, 35-cm-long piece of wood (Fig. 1). The can was secured by a wood screw and washer and sprayed with two coats of gloss white enamel paint (#745-3013, Martin-Senour Paints, Cleveland, Ohio). A wood stake was driven into the ground and a trap was wired to the stake with the trap top 75 cm above ground level. After assembly, a plastic bag (20 × 10 × 46 cm) smeared with Stikem Special (Michel Pelton Co., Emeryville, California) in the inside was inverted over the can to expose the sticky surface. Each trap presented 1056 cm^2 of sticky white surface area. Traps were positioned in pairs 10 m apart within and around the pastures occupied by cattle. One of each pair was adjacent to fresh dung. The other was at least 3 m removed from dung. Traps were usually assembled at sunrise (7) and dismantled between 1300 and 1700 PDST.

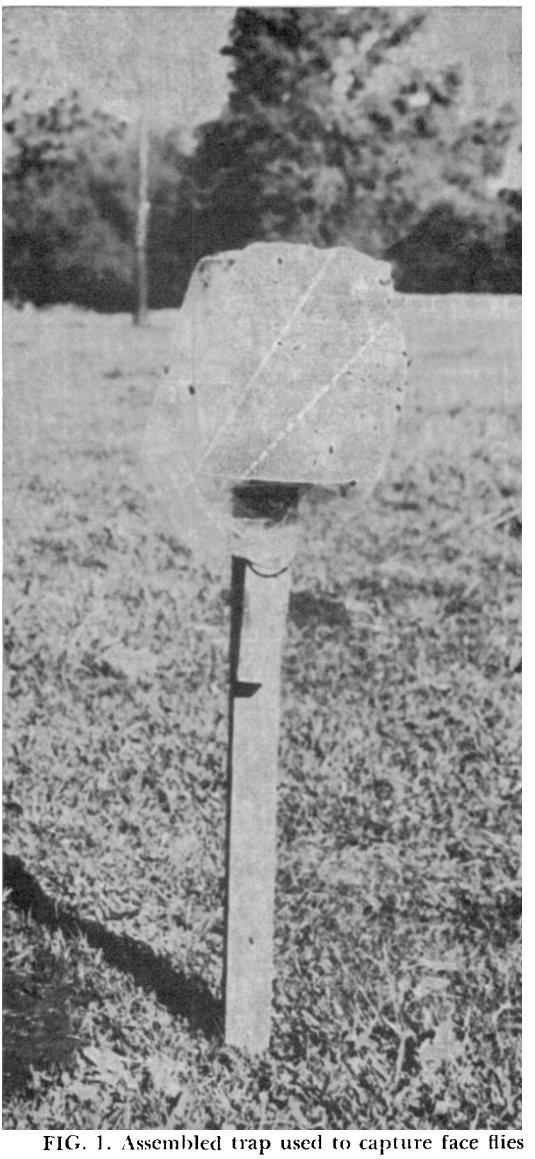

FIG. 1. Assembled trap used to capture face flies in pasture.

The time and air temperature were recorded at sunrise and again at the end of each collection interval. The sampling dates and numbers of traps are summarized in Table 3.

Indices of adult fly abundance were derived from each trap by dividing the total female flies by the hours that each trap was in operation, and then correcting for the effects of air temperature (Moon and Kaya, in prep.). A second independent index of abundance was made by counting the flies seen feeding at faces of cattle resting in shade (3).

Face flies were collected from each trap every 1–3 h, washed in xylene or paint thinner for 10–15 min to remove the Stikem, rinsed in 70% ethanol, and then placed in 0.1% formalin-Ringer's solution. Flies from each collection were held at 4 C for 1–2 days and dissected in Ringer's solution under a stereomicroscope. In fall and winter, diapausing flies were collected from the attic of the ranch house and dissected.

The following information was noted: sex, gut contents, presence or absence of nematodes, stages of nematode present, and status of fat body and ovaries of infected and healthy females. Flies were categorized according to gut contents. Blood and dung were immediately recognizable. Other substances found in the gut were creamy, brown, or yellow in color. In some cases, the gut appeared clear or empty. Infected female flies were classified into one of four nematode age classes: 1) gamogenetics only; 2) parthenogenetics; 3) gamogenetic juvenile males and females in the hemocoel; and 4) ovaries noticeably distended with gamogenetic male and female nematodes. Class 4 flies were assumed to be capable of nemapositing.

Uninfected female flies were classified into 1 of 11 physiological age classes by the condition of the fat body and ovaries (5). Females were categorized as newly emerged (N-0) if pupal fat body was present, and nulliparous (N-1 to N-5) or parous (P-6 to P-10) if yellow follicular relics were respectively absent or present in the lateral oviducts. Uniparous, biparous, and triparous flies could not be distinguished with confidence; hence all were considered parous (16). Within each stage of parity, follicular development ranged from early (N-1 and P-6) to late (N-5 and P-10) stages of egg maturity.

The distribution and abundance of healthy and infected face flies in dung were studied by exposing pats to wild flies at known times of the day and night in selected locations receiving either full sun, partial sun, or shade during the day within the Yuba County ranch. Fresh dung was collected within minutes of defecation but before face flies could visit it. Dung from 10–20 animals was pooled, mixed, and divided into 800 ± 20-g portions. Each portion was placed on a 25-cm^2 sheet of plastic and reconstructed to resemble a natural dropping. All artificial pats remained exposed to insect activity for 48–72 h. Then the pats were transferred individually onto sand in 25-cm-diam trays, covered with gauze and hardware cloth, and held in a greenhouse until the dung inhabitants pupated. Fly puparia were sifted from the sand, and samples of face flies from each pat were placed in ventilated snap-cap vials. Emerging adults were dissected, and the gamogenetic nematodes were counted. Thus the frequency of hosts, and of nematodes within each host, was obtained for each pat. Additionally, when artificial pats were not exposed, natural pats were collected and processed as above. Table 2 summarizes the number of pats collected on each sampling date.

Observed infection rates in flies emerging from artificial and natural pats were compared with infection rates of "new" flies (N-0 + N-1) collected on traps one larval-pupal development time after each set of pats was exposed. Regression analysis was used to investigate factors which affected infection rates.

The frequency distribution of gamogenetic *H. autumnalis* within face flies was tested for randomness by comparing observed frequencies with those predicted by a Poisson distribution. Males and females from dung were analyzed separately. The influence of nematodes on host behavior was analyzed by chi-square analysis of age classes and gut contents.

RESULTS AND DISCUSSION

Surveys in northern California: Heterotylenchus autumnalis was present in all face fly populations sampled, with occurrence in the flies collected ranging from 4.7% to 43.8% (Fig. 2). This extends the known distribution of *H. autumnalis* to California.

Within-pasture distribution of host and nematode: Data were analyzed from artificial and natural pats exposed in full sun, partial sun, and full shade during day and night within the Yuba County ranch in 1977. No significant differences in the frequency of fly infestation or nematode infection were found between natural and artificial pats exposed on the same dates. Host population density and infection rate

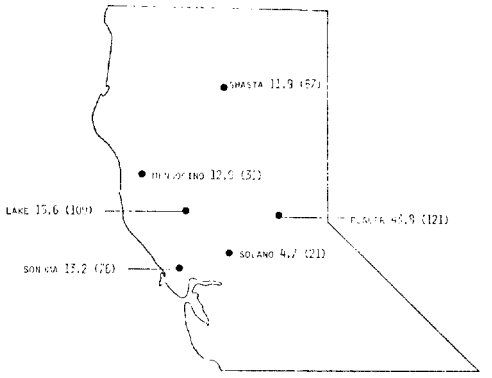

FIG. 2. Percent face flies infected with *Heterotylenchus autumnalis* in 6 counties in northern California in 1977. Number of flies dissected shown in parentheses.

varied with exposure of pats to sunlight (Table 1). No face flies were found in pats exposed in day-long shade. This result was too consistent to be explained by mortality in immature stages. Forty percent of pats in partial sun (1/3 to 2/3 day-length) and 75% of pats in full sun (> 2/3 day-length) were infested. Both host population density and percent infection were highest in pats in full sun.

We assessed the influence that time of dung deposition during night (2400 PDST) or day (0600, 1200, 1800 PDST) had on the rates of infestation and infection of artificial pats under full and partial sun exposure. Rates of fly infestation were 84.1% (n = 63) and 76.3% (n = 211) in pats exposed during night and day respectively. Of pats which were infested and yielded viable adults, 51.5% (n = 47) of night pats and 64.4% (n = 146) of day pats yielded infected adults. Fly infestation rates and nematode infection rates from night and day pats were not significantly different ($P > 0.10$). Thus, dung deposited at night remained attractive to the diurnally active flies the following morning, and the probability of a pat receiving eggs and nematodes was affected by exposure to direct sun. Partially shaded pats appeared marginally attractive to ovipositing and nemapositing face flies. Experiments with caged flies presented by Teskey (14) showed that females lay more eggs in dung in full sun than in shade. Our results confirm his findings.

Frequency of nematodes within hosts: Over 3,000 flies from the 11 sampling dates (Table 2) were collected from dung in all locations and dissected to assess infections. Sex ratios or percent infection between sexes were not significantly different ($P > 0.05$). Fifteen samples provided sufficient data to assess the frequency distribution of nematodes within hosts. Seven of eight samples of males and seven samples of females differed considerably from the Poisson distribution. Individuals bearing one or two gamogenetic nematodes were less frequent than expected; healthy individuals and those bearing three or more (up to 26) nematodes were more frequent than expected. Thus the frequency distribution of nematodes within face flies was not random; superinfections were common. Similar findings were reported by Thomas et al. (16).

Two hypotheses may explain the observed distribution: 1) larvae may be

TABLE 1. Distribution of face fly larve and *Heterotylenchus autumnalis* in natural and artificial cow pats collected from three habitats within ranch in Yuba County, California, 1977.

Location	Number of cow pats[a]			Mean number of puparia per pat	% of flies infected by nematodes[c]
	Collected	Infested with			
		Flies	Nematode-infected flies[b]		
Full shade	99	0	—	—	—
Partial sun	63	25	13	13.5	13.1
Full sun	302	227	143	105.7	38.6

[a]Forty-six pats in full sun were natural droppings of unknown weight. All others were reconstructed from fresh dung and weighed 800 ± 20 g.
[b]Pats produced at least one nematode-infected fly.
[c]Weighted by pupal density within all pats with and without nematode-infected flies.

TABLE 2. Summary of face fly samples collected from cattle dung exposed in pastures of ranch in Yuba County, California, 1977.

Date	No. pats[a]	Pats with puparia	$\bar{x}$ puparia ± SE[b]	Date of adult emergence[c]	Pats with infected flies[d]	% infection (♂ + ♀)[e] Pats with infected flies (n)	% infection (♂ + ♀)[e] All pats (n)
5/22	40 (A)	40	399.3 ± 33.6	6/5	39	52.7 (488)	52.7 (493)
6/4	40 (A)	40	150.0 ± 18.4	6/16	21	38.1 (153)	26.2 (238)
6/21[f]	10 (N)	7	8.5 ± 5.3	6/29	6	48.7 (47)	40.3 (55)
7/1	28 (A)	25	29.8 ± 6.0	7/12	17	23.8 (255)	22.4 (289)
7/14[f]	20 (N)	13	15.7 ± 6.7	7/23	6	42.3 (158)	35.9 (184)
7/25	32 (A)	26	25.1 ± 6.3	8/2	7	7.2 (168)	4.3 (408)
8/5	16 (N)	11	22.6 ± 11.9	8/16	7	4.9 (143)	4.5 (170)
8/17	38 (A)	22	34.3 ± 10.3	8/27	13	20.9 (227)	17.7 (339)
9/1	48 (A)	36	51.1 ± 8.4	9/9	23	20.2 (811)	16.0 (1,043)
9/15	40 (A)	3	0.1 ± 0.1	10/3	0	— —	— —
9/22	30 (A)	7	2.0 ± 0.8	10/8	4	46.5 (28)	25.1 (54)
10/1	16 (A)	0	0.0 ± —	—	—	— —	— —
10/9	26 (A)	0	0.0 ± —	—	—	— —	— —

[a](A) = artificial pats formed from 800 ± 20 g fresh cow dung; (N) = natural pats of unknown weight. All pats exposed in locations receiving full sun all day.
[b]Total pupae divided by total no. pats exposed.
[c]Estimated from day-degrees above 12.9 C accumulated in dung from date of exposure.
[d]Pats produced at least one infected fly.
[e]Estimate weighted by pupal density within pats.
[f]Pats may not have been exposed to full day's fly activity and insolation.

differentially susceptible to the nematode because of genotype or age; or 2) nematodes or face fly eggs or both may be distributed by the female flies in clumps. Female flies are known to deposit eggs singly, but as the surface of each pat dries and a crust forms, oviposition is restricted to cracks and crevices on the surface (1). This drying process may cause aggregations of eggs and nematodes. Eggs and nematodes deposited before the dung surface dries may be dispersed sufficiently to reduce contact between host and nematode.

Comparison of the number of gamogenetic nematodes per host and the percent infection across all pats for each date revealed a highly significant correlation between the two ($n = 18$, $r = 0.95$). The percent infection and number of gamogenetic nematodes per host increase together. The factor(s) which regulate the two require further research.

Effects of H. autumnalis on face fly: Of 1,252 flies old enough to show signs of maturing eggs (age classes N-2 to P-10), one was infected. Of 273 flies containing nematodes (classes 3 and 4), three possessed follicular relics indicating completion of at least one gonadotrophic cycle. Therefore, it seems that the great majority of nematode-infected flies in the field fail to produce any eggs. In contrast, Treece and Miller (17) found that laboratory-reared females with nematodes completed their first egg cycle before becoming sterile. Our data suggest that infected females should be considered sterile upon emergence. Infected females may differ from uninfected females in feeding behavior (Fig. 3). Flies with juvenile male and female nematodes in their hemocoel (classes 3 and 4) were rarely found with blood in their digestive tracts. Uninfected females of about the same age fed more frequently on blood ($P < 0.01$). Dung feeding was less frequent in classes 1 and 2 and more frequent in class 4 infected flies than in their uninfected counterparts ($P < 0.01$). However, both infected and uninfected flies of all ages fed with similar frequency on the "creamy" substance ($P > 0.05$). While the identity of this material is not confirmed, we believe it is of animal origin. If "creamy" is material acquired from faces of cattle, then infected and uninfected flies of common physiological age feed on the animals with equal probability. Substances found in the gut less frequently were classified as yellow, brown or clear.

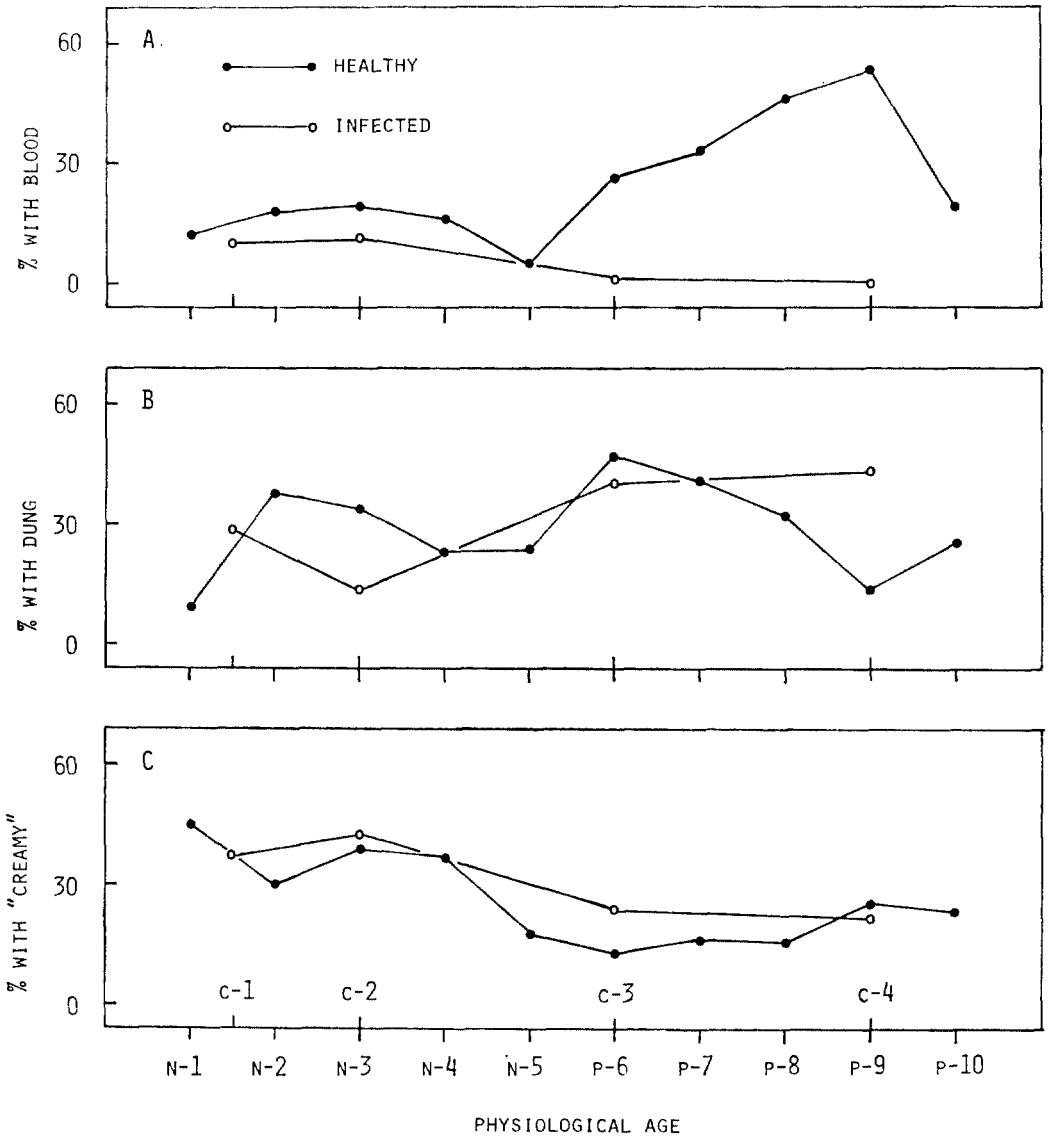

FIG. 3. Percent healthy and nematode-infected female face flies of different physiological ages collected in 1977 with identifiable food substances in their digestive tract. N-1 to P-10 are healthy females. C-1 to C-4 (class 1 to class 4) refers to infected females. Age classes approximated from Miller and Treece (4) and Treece and Miller (17).

These substances, of unknown origin, may have been obtained from vegetation (1).

Seasonal dynamics of face fly and H. autumnalis in Yuba County: Estimates of infection were independent of sampling methods. Because males spend less time in open pasture (14), they were undersampled on the white traps. Therefore, results for trapped flies were based only on female flies. Additionally, no significant differences in percent nematode infection of females captured occurred between dung traps and no-dung traps. Hence data from both types of traps were combined. The relative merits and efficiencies of the different methods of sampling from larval and adult face fly populations will receive detailed discussion elsewhere (Moon and Kaya, in prep.).

Both indices of adult face fly abundance showed that fly populations were highest in late May, declined to a midsummer low in early August, and reached a second peak, much smaller, by October 1 (Table 3). Flies then disappeared as they entered diapause

and left the pastures. The frequency of nulliparity was highest at the start of the season (85%), declined linearly until mid-September (20%), and then rose abruptly to 100% for the remainder of the season. The first definitive signs of diapause were noted in the October 1 samples. These females possessed undeveloped ovaries and a hypertrophied fat body. Diapause was first initiated in newly emerged flies 1–2 weeks earlier; thus the September-October peak was composed mostly of females which eventually entered diapause.

Incidence of nematode infection in females of all ages was highest (18–41%) from late May through mid-July, when face fly populations were high (Table 3). The infection rate fluctuated between 6 and 13% from mid-July to early October and then increased slightly in mid-October. The infection rates in samples of diapausing adults from the ranch house attic during fall and winter agreed with those observed in field-collected flies in the last half of October (Table 3). Infection rates in diapausing males and females were not significantly different from each other. Only gamogenetic and parthenogenetic nematodes were present in both sexes of diapausing flies.

Pupal densities from artificial pats declined exponentially from May 22 to July 25, and then increased until September 1 (Table 2). Densities were essentially zero in pats exposed on and after September 15. Data from natural pats were not consistent with data from artificial pats. In part, differences may be attributed to length of exposure in the field and other uncontrolled factors.

As estimated from artificial pats, the rate of nematode infections in new flies entering the population declined from 52.7% on June 5 to 7.2% on August 2, and rose to 25% at the end of emergence around October 8 (Table 2). A comparable fluctuation occurred in "new" flies trapped during the season (Table 3). The infection rate of all ages exhibited the same pattern, but lagged 5 to 15 days behind that of "new" flies (Table 3).

In California, as in Nebraska (2) and Mississippi (9), infection rates in new flies declined in late spring through the summer

TABLE 3. Summary of estimates of adult face fly abundance and incidence of *Heterotylenchus autumnalis* infection in Yuba County, California, 1977.

Date	Females/ trap x hour ± SE[a]	No. traps	Flies/face ± SE	% females infected: Newly emerged (n)[b]	% females infected: All ages (n)
5/22	52.8 ± 7.4	6	60.0 ± 6.3	30.0 (10)	23.3 (301)
6/4	22.0 ± 4.3	6	22.0 ± 5.1	22.2 (9)	40.6 (175)
6/21	36.4 ± 2.9	6	20.2 ± 3.0	20.4 (54)	34.8 (276)
7/1	11.4 ± 2.8	10	13.4 ± 2.3	38.5 (78)	27.2 (497)
7/14	10.2 ± 1.6	10	5.3 ± 1.1	30.4 (23)	18.4 (179)
7/25	5.5 ± 1.4	10	2.8 ± 0.6	17.1 (41)	11.0 (210)
8/5	1.4 ± 0.3	10	0.7 ± 0.3	0.0 (5)	7.8 (51)
8/17	2.8 ± 0.7	10	0.8 ± 0.2	25.0 (8)	12.9 (101)
9/1	3.4 ± 0.9	10	4.7 ± 0.8	6.3 (32)	8.6 (185)
9/15[c]	2.6 ± 0.4	6	1.8 ± 0.3	26.5 (34)	10.7 (112)
9/22	2.1 ± 0.4	10	2.9 ± 0.5	1.6 (63)	6.7 (135)
10/1	5.2 ± 1.3	6	7.0 ± 0.8	4.5 (112)	5.8 (173)
10/9	1.9 ± 0.7	10	5.8 ± 1.0	11.6 (43)	10.3 (68)
10/14	0.2 ± 0.1	10	1.8 ± 0.5	28.6 (7)	22.2 (9)
10/22	0.9 ± 0.3	10	2.2 ± 0.6	13.8 (29)	15.2 (33)
10/22[d]	—	—	—	— —	18.8 (16)
11/2	0.1 ± 0.1	10	0.5 ± 0.2	33.3 (3)	25.0 (4)
11/2[d]	—	—	—	— —	13.3 (30)
12/30[d]	—	—	—	— —	23.7 (59)

[a]Total females trapped per hour trap effort after sunrise and at 15 C (see 7).
[b]Age classes N-0 and N-1, and infected class 1.
[c]Windy and cloudy by 1000 h PDST.
[d]Females collected from attic of ranch house.

and increased in the fall. To explain the midseason decline in infection, Jones and Perdue (2) proposed the hypothesis that infection rates decrease as face fly larval developmental rate increases. That is, the decline is caused by warmer dung temperatures in summer, and the rise in fall occurs as dung temperatures decrease. However, infection rates may not be related to differential development of face fly and nematode. Higher dung temperatures may directly kill the nematodes or render them uninfective. Further experimentation is required to clarify the mechanism(s).

Previous workers have concluded that *H. autumnalis* is an important agent controlling face fly (15, 16), a plausible conclusion in view of the effect of the nematode on its reproduction. If a direct density-dependent relationship exists, percent infection should be higher in pats with higher larval densities. Comparisons were made among pats exposed on the same day. Attention was restricted to pats yielding at least one infected fly (male or female). Infection and density were related directly only in two of the ten samples. The remainder showed density independence. An inverse density-dependent relationship is possible, but variation within the samples was too large to permit this conclusion. Our data do not support the hypothesis that *H. autumnalis* regulated face fly in Yuba County in 1977. The extent to which *H. autumnalis* controlled face fly could not be assessed. That would require an experimental check, which is not possible with present field methods.

Attempts failed to increase infection rates above 30% in laboratory colonies (2). There appears to be a mechanism which limits the infection of *H. autumnalis* in face fly populations. We compared the infection rates in females (class 4 and age class N-5 and P-10) that visited dung (parents) with rates observed in flies reared from pats exposed to visiting females on the same day (progeny). The infection rate of progeny was related ($P = < 0.01$; $b = 0.446$; $r^2 = 0.61$) to that of parents for the ten sampling dates between May 22 and September 22 (Fig. 4). The intercept is not significantly different from the origin. Infection rates in progeny were less than half the rates in parents. Possibly, superinfections noted earlier may be involved in restricting transmission of *H. autumnalis*, but other mechanisms may also be involved. Efforts to increase infection rates by releasing infected flies would be most profitable when infection rates in field populations are low, and least profitable when they are high.

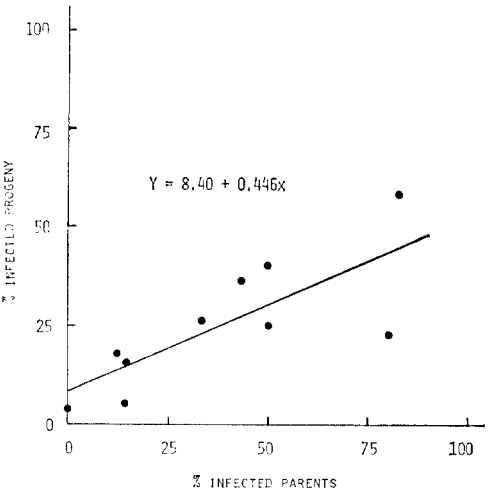

FIG. 4. Relationship between infection rates in parent face flies visiting cow pats and infection rates in progeny reared from the same pats on 10 different days during 1977.

LITERATURE CITED

1. HAMMER, O. 1942. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. Vidensk. Med. Dansk. Naturh. Foren., Kbh. 105:141-393.
2. JONES, C. M., and J. M. PERDUE. 1967. Heterotylenchus autumnalis, a parasite of the face fly. J. Econ. Entomol. 60:1393-1395.
3. McGUIRE, J. V., and R. I. SAILER. 1962. A method of estimating face fly populations on cattle. USDA Agr. Res. Serv. 33-80. 8 pp.
4. MILLER, T. A., and R. E. TREECE. 1968. Some relationships of face fly feeding, ovarian development, and incidence on dairy cattle. J. Econ. Entomol. 61:250-257.
5. MILLER, T. A., and R. E. TREECE. 1968. Gonadotropic cycles in the face fly, Musca autumnalis. Ann. Entomol. Soc. Amer. 61: 690-696.
6. NICKLE, W. R. 1967. Heterotylenchus autumnalis sp. n. (Nematoda: Sphaerulariidae), a parasite of the face fly, Musca autumnalis De Geer. J. Parasitol. 53:398-401.
7. ODE, P. E., and J. G. MATTHYSSE. 1967. Bionomics of the face fly, Musca autumnalis De Geer. N. Y. Agric. Exp. Sta., Ithaca. Mem. 402. 91 pp.
8. PICKENS, L. G., R. W. MILLER, and J. J.

GRASELA. 1977. Sticky panels as traps for Musca autumnalis. J. Econ. Entomol. 70: 549-552.

9. ROBINSON, J. V., and R. L. COMBS, JR. 1976. Incidence and effect of Heterotylenchus autumnalis on the longevity of face flies in Mississippi. J. Econ. Entomol. 69:722-724.
10. STOFFOLANO, J. G., JR. 1967. The synchronization of the life cycle of diapausing face flies, Musca autumnalis, and of the nematode, Heterotylenchus autumnalis. J. Invertebr. Pathol. 9:395-397.
11. STOFFOLANO, J. G., JR. 1968. Distribution of the nematode Heterotylenchus autumnalis, a parasite of the face fly, in New England with notes on its origin. J. Econ. Entomol. 61:861-863.
12. STOFFOLANO, J. G., JR. 1970. Parasitism of Heterotylenchus autumnalis Nickle (Nematoda, Sphaerulariidae) to the face fly, Musca autumnalis De Geer (Diptera: Muscidae). J. Nematol. 2:324-329.
13. STOFFOLANO, J. G., JR., and W. R. NICKLE. 1966. Nematode parasite (Heterotylenchus sp.) of face fly in New York State. J. Econ. Entomol. 59:221-222.
14. TESKEY, H. J. 1969. On the behavior and ecology of the face fly, Musca autumnalis (Diptera: Muscidae). Can. Entomol. 101:561-576.
15. THOMAS, G. D., and B. PUTTLER. 1970. Seasonal parasitism of the face fly by the nematode Heterotylenchus autumnalis in central Missouri, 1968. J. Econ. Entomol. 63: 1922-1923.
16. THOMAS, G. D., B. PUTTLER, and C. E. MORGAN. 1972. Further studies of field parasitism of the face fly by the nematode Heterotylenchus autumnalis in central Missouri, with notes on the gonadotrophic cycles of the face fly. Environ. Entomol. 1:759-763.
17. TREECE, R. E., and T. A. MILLER. 1968. Observations on Heterotylenchus autumnalis in relation to the face fly. J. Econ. Entomol. 61:454-456.