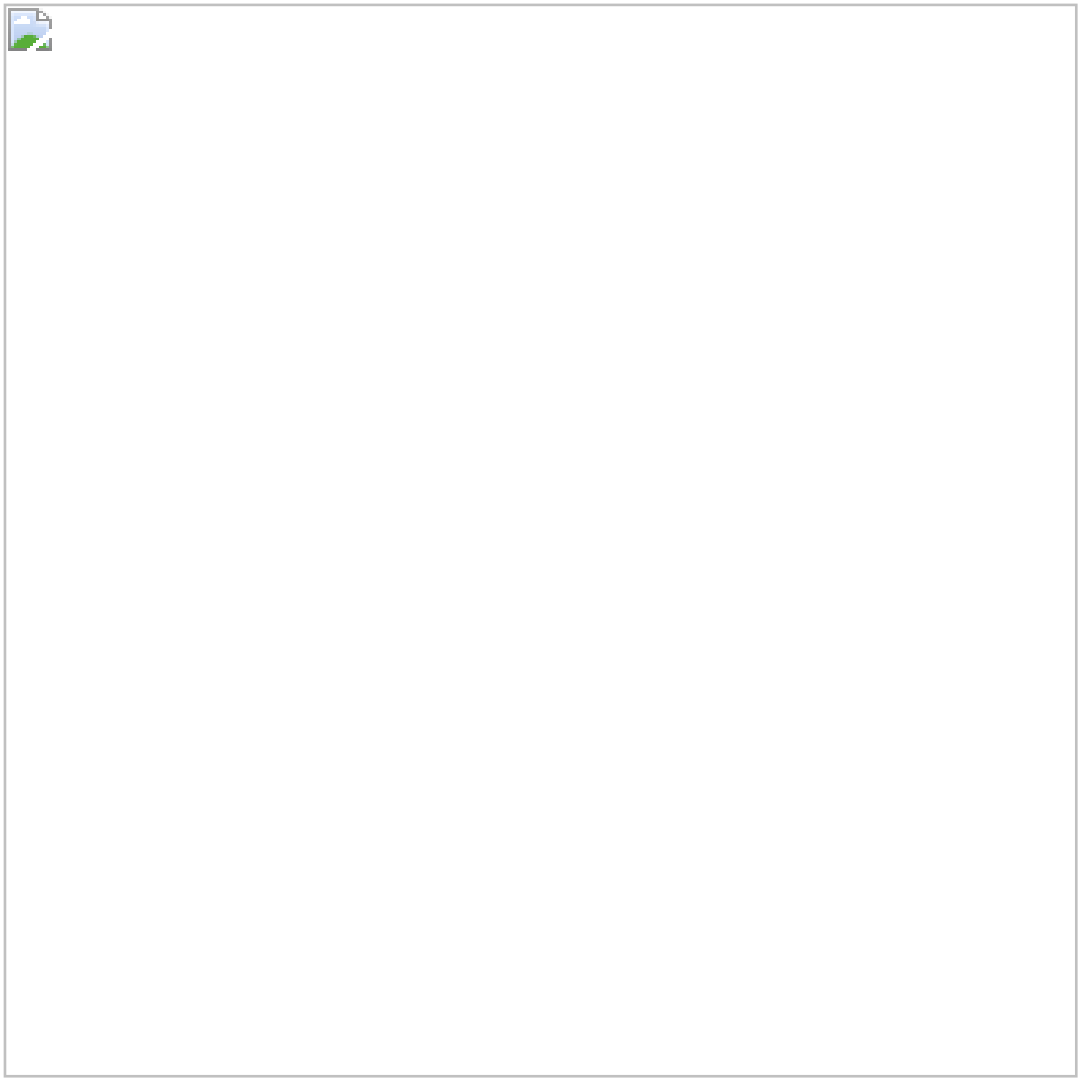

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SEASONAL PREVALENCE OF *TAENIA TAENIAEFORMIS*: RELATIONSHIP TO AGE, SEX, REPRODUCTION AND ABUNDANCE OF AN INTERMEDIATE HOST (*PEROMYSCUS MANICULATUS*)

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ABSTRACT: Livers from 4,501 deer mice (*Peromyscus maniculatus*) collected from a weedy habitat in northeastern California during 48 consecutive monthly samplings were examined microscopically for *Taenia taeniaeformis* larva. Although there were pronounced seasonal fluctuations in host density, there were no significant annual or season-related differences in cestode intensities in adult deer mice. There were no significant differences in prevalences associated with sex of the host, nor were there significant changes in level of reproduction noted between infected and non-infected hosts. There were, however, significant differences in prevalences between young (1.2%) and adult (4.2%) hosts. Plausible mechanisms for this age-related difference in prevalence rates include (1) differential susceptibility due to the activity pattern of adult mice and/or (2) passive immunity in neonates as a result of colostrum- and/or transplacentally-transferred immunoglobulins and (3) capture of subadult animals before they had completed the period of highest susceptibility to *T. taeniaeformis*. Density of larvae per mouse liver was determined during a 21 mo consecutive period. The intensity of *T. taeniaeformis* larvae was not significantly different between the sexes of the adult mice. The larval stage showed an overdispersion pattern within the adult population. These results suggest that determinations of *T. taeniaeformis* abundances can be accurately made, at least in this *P. maniculatus* population, at any time of the year provided adjustment is made for the relative age structure of the host population.

Key words: Cyclophyllidean tapeworm, *Taenia taeniaeformis*, *Peromyscus maniculatus*, prevalence, intensities, abundances, host age/sex structure, annual cycles, field study, differential susceptibility.

INTRODUCTION

Predator-prey interactions are utilized by a wide variety of tapeworms by which the intermediate host stage is transferred to the definitive host. For example, adult *Taenia taeniaeformis*, a cyclophyllidean tapeworm found in the small intestine of a variety of carnivorous definitive host species, utilizes rodents as an intermediate host. In this case, gravid proglottides passed in the feces of definitive hosts contain ova infective to intermediate hosts. These ova are passed to the intermediate host via direct ingestion of the feces or by ingesting ova freed from disintegrating proglottides in the external environment. Thus, population levels of this parasite may be affected by densities of both the definitive and intermediate hosts as well as by density independent meteorological/geological factors.

In the present study we report the seasonal prevalences and intensities of *T. taeniaeformis* in the livers of an intermediate host, the deer mouse (*Peromyscus maniculatus*), and the association of these levels to the age, sex, reproductive status, and relative abundance of the host.

MATERIALS AND METHODS

The deer mice examined during this study were captured from weedy ditch banks along dike roads on the Tule Lake National Wildlife Refuge (Siskiyou County, California USA; 41°50'N, 121°30'W) at an elevation of 1,230 m. The study area, 40 m wide and 7 km long, is bounded along the long axis by Tule Lake on one side and by an irrigation ditch on the other. Both ends are bounded by dirt roads and noncontiguous habitats. The most prominent weedy

TABLE 1. Prevalence of *Taenia taeniaeformis* larva in the livers of 3,182 adult deer mice *Peromyscus maniculatus gambelii*.

	1985				1986				1987				1988			
	M		F		M		F		M		F		M		F	
	N*	L*	N	L	N	L	N	L	N	L	N	L	N	L	N	L
JAN	10	0	10	0	54	3	29	2	44	1	45	5	26	0	20	0
FEB	34	1	27	0	71	3	28	3	41	0	31	1	48	0	41	0
MAR	45	1	37	2	56	4	33	0	39	2	31	0	51	4	36	4
APR	27	1	55	2	50	3	45	2	36	3	31	1	53	5	49	1
MAY	33	1	26	0	38	1	50	2	34	3	32	1	38	4	12	1
JUN	38	0	46	0	29	0	73	3	39	0	56	2	18	2	29	3
JUL	25	2	39	0	21	1	45	3	38	0	48	2	21	1	30	0
AUG	17	1	18	2	10	1	22	1	19	0	31	1	17	3	19	0
SEP	22	4	27	1	20	0	40	2	13	0	19	1	15	0	23	0
OCT	28	4	29	1	23	2	33	1	23	0	23	1	22	1	11	0
NOV	40	3	22	0	32	4	23	3	44	1	28	1	21	0	19	0
DEC	30	1	23	1	103	2	92	1	13	0	13	0	26	2	18	0

* Given monthly for each sex is the total number of livers examined (N) and the number containing one or more larva (L).

vegetation in the ditch-bank habitat consists of summer-cypress (*Kochia scoparia*), tansy-mustard (*Descurainia Sophia*), tumble-mustard (*Sisymbrium altissimum*), giant wildrye (*Elymus cinereus*), lamb's quarters (*Chenopodium album*) and nettle, (*Urtica holosericea*). The vegetation forms a dense cover during the spring and early summer but by the fall and winter seasons the area is only sparsely covered by dead plants consisting primarily of nettle and mustard.

The climatic conditions of the study area are characterized by warm dry summers and relatively cold winters during which most of the usually low amount of annual precipitation occurs. Frost can occur during any month of the year. Daily photoperiods (sunrise to sunset) range from about 15 hr in June to 9 hr in December. Daily values for meteorological conditions which occurred during the four years of this study are on file at Refuge Headquarters (Tule Lake National Wildlife Refuge, Tule Lake, California 96134, USA).

All mice were captured in rolled oat-baited Sherman live traps spaced at 8 m intervals along sections of the dike roads. Trapping was conducted at the new moon phase of each lunar cycle from January 1985 through December 1988. Deer mice captured during the 48 consecutive months of this study were killed, weighed, measured, and sex and reproductive status determined. They were then classified as adult (body length ≥90 mm) or as subadult (body length <90 mm). Use of body length as a criterion of age class is consistent with other age-related characteristics in this population of deer mice such as the nature of the pelage and reproductive maturity. The liver was removed intact from each animal, fixed in 10% formalin, and examined under a dissecting microscope for the presence of *T. taeniaeformis* larva. From April 1987 through December 1988 the numbers of strobilocerci in each infected liver were counted.

RESULTS

General

The 4,501 deer mice captured during 48 consecutive monthly trapping periods beginning January 1985 were examined for the presence of *T. taeniaeformis* larva in the liver. The adult population consisted of 1,608 male and 1,574 female mice (Table 1), the subadult population consisted of 755 male and 564 female mice (Table 2). Since no sex-related difference (χ^2 = ≤3.50 adult; ≤3.09 subadult, $P > 0.05$, 1 df) in *T. taeniaeformis* infection occurred in any monthly sample within either age class, the sexes were grouped for subsequent analysis. Total prevalence of *T. taeniaeformis* infected livers was significantly greater ($\chi^2 = 25.26$, $P < 0.001$, 1 df) in adult (130 of 3,182 = 4.1%) than in subadult mice (16 of 1,319 = 1.2%). Significantly greater prevalence of *T. taeniaeformis* infection in the adult component of the population occurred during

TABLE 2. Prevalence of *Taenia taeniaformis* larva in the livers of 1,319 subadult deer mice *Peromyscus maniculatus gambelii*.

	1985				1986				1987				1988			
	M		F		M		F		M		F		M		F	
	N*	L*	N	L	N	L	N	L	N	L	N	L	N	L	N	L
JAN	0		0		11	0	21	0	7	0	9	0	4	0	1	0
FEB	5	0	6	0	7	0	12	0	8	0	20	0	6	0	7	0
MAR	9	0	9	0	8	1	26	0	14	0	16	0	12	0	6	0
APR	11	0	6	0	2	0	11	0	18	0	23	0	13	0	12	0
MAY	17	0	22	1	5	0	10	0	14	0	24	0	24	1	7	1
JUN	8	0	8	0	3	0	2	0	5	1	6	1	12	0	7	0
JUL	13	0	5	0	21	0	13	0	10	0	6	0	4	0	0	—
AUG	41	0	22	0	47	0	19	0	38	0	12	0	16	0	4	0
SEP	36	0	15	0	37	1	6	0	51	0	14	0	13	1	5	0
OCT	22	0	21	0	41	2	10	0	17	0	14	0	11	0	8	0
NOV	15	2	23	0	32	1	32	0	20	0	8	0	5	0	4	0
DEC	20	1	27	2	9	0	15	0	7	0	6	0	6	0	4	0

* Given monthly for each sex is the total number of livers examined (N) and the number containing one or more larva (L).

1985 ($\chi^2 = 4.08$, $P < 0.05$), 1986 ($\chi^2 = 9.18$, $P < 0.01$) and 1987 ($\chi^2 = 7.99$, $P < 0.01$). Prevalence during 1988, although numerically higher in the adult component, was not significantly greater than in the subadult age class ($\chi^2 = 3.74$). Because of the overall greater prevalence of *T. taeniaeformis* among adults, analysis of seasonal and annual prevalence of *T. taeniaeformis* infection was made on each age class.

Prevalence parasite relative to host age class

Annual prevalence of *T. taeniaeformis* infection in adult deer mice during this study averaged 4.2% and did not vary significantly between years ($\chi^2 = 3.76$, $P > 0.05$, 3 df); nor were there significant differences ($P > 0.05$, 3 df) in infection levels between seasons during 1986 ($\chi^2 = 1.05$), 1987 ($\chi^2 = 1.82$), and 1988 ($\chi^2 = 7.41$). In contrast, a significant ($\chi^2 = 8.41$, $P < 0.05$, 3 df) season-related difference in prevalence of *T. taeniaeformis* occurred during 1985 when the combined prevalence for winter-spring averaged 2.1% (eight of 388) and was significantly lower ($\chi^2 = 7.87$, $P = 0.01$, 1 df)) than the combined prevalence for summer-fall which averaged 6.3% (20 of 320).

The annual prevalence of *T. taeniaeformis* infection in the livers of subadult deer mice averaged 1.2% during this study and did not vary significantly between years ($\chi^2 = 2.25$, $P > 0.05$, 3 df). Seasonal infection levels were not statistically different from each other over the grouped years ($\chi^2 = 6.78$, $P > 0.05$, 3 df).

Prevalence of parasite relative to host reproductive status

Essentially half of the 1,574 adult females (789, 50.1%) captured during this study were reproductively active. The seasonal levels of reproduction for each year of the study are given in Table 3. The contribution of *T. taeniaeformis*-infected and non-infected individuals (relative to their respective proportion of the total population) to the numbers of reproductively active and reproductively quiescent adult female deer mice was examined for each season of each year of the study. In no case was there a significant difference ($\chi^2 = \leq 2.20$, $P > 0.05$, 1 df) in pregnancy of adult female deer mice related to the presence or absence of *T. taeniaeformis* in the liver of the host animal; nor were there significant *T. taeniaeformis*-related differences ($\chi^2 = \leq 2.41$, $P > 0.05$, 1 df) when seasons were grouped by years.

TABLE 3. Seasonal levels of deer mouse reproduction expressed as a percent of adult females examined (N) that were pregnant and/or lactating.

	Winter		Spring		Summer		Fall	
	N	%	N	%	N	%	N	%
1985	74	52.7	127	33.8	84	59.5	74	25.7
1986	90	2.2	168	41.1	107	93.5	148	48.0
1987	107	35.5	119	31.1	98	91.8	71	67.6
1988	97	55.6	90	47.8	72	91.7	48	41.7
Total	368		504		361		341	
Average		36.1		38.1		84.4		46.3

Relationship of parasite to host relative abundance

The relative abundance of deer mice expressed as the average number of mice captured per 100 traps during each 3 month season of each year of the study is given in Table 4. The relative abundance levels exhibited considerable seasonal variation within years as well as in total abundance between years. The greatest fluctuation of seasonal host abundance within a single year occurred during 1987 when winter levels of 94.1% fell to 10.9% during the summer. The prevalences of *T. taeniaeformis* larvae (winter = 3.9%, summer = 2.4%) were not significantly different ($\chi^2 = 0.71$, $P > 0.05$, 1 df) between the two seasons. The extreme seasonal difference in host abundance over the entire study occurred between spring 1985 (97.7%) and summer 1987 (10.9%). However, the prevalences of *T. taeniaeformis* larvae during these seasons (1.8% and 2.4% respectively) were not significantly different ($\chi^2 = 0.17$, $P > 0.05$, 1 df) from each other. Further, although annual host abundance ranged from 84.3% in 1985 to 28.5% during 1988, the *T. taeniaeformis* prevalence levels during these years (4.0% versus 4.7%) were not significantly different ($\chi^2 = 0.43$, $P > 0.05$, 1 df). Thus, it appears that in this host-parasite association, the degree of numerical fluctuation of the intermediate host population had little effect on the overall prevalence rate of the parasite.

TABLE 4. Relative abundance of deer mice expressed as number of captures per 100 live traps, expressed as averages for each 3 mo season and annual averages for 1985 to 1988.

	Winter	Spring	Summer	Fall	Annual
1985	84.5	97.7	94.8	60.0	84.3
1986	61.3	38.8	15.7	32.8	37.2
1987	94.1	42.4	10.9	20.7	42.0
1988	34.3	39.7	15.3	24.6	28.5
1985–88	68.5	54.7	34.2	34.5	48.0

Relationship of host sex and age and season to parasite intensities

Table 5 shows the intensities of strobiloceri in all deer mice caught from April

TABLE 5. Level of infection of strobiloceri (number of cysts) determined from the livers of 615 adult male and 588 adult female deer mice collected on a monthly basis from April 1987 through December 1988. Given are the numbers of mice of both sexes at various levels of infection (number) and the percentage (%) of the total number of mice examined.

Cysts Number	Male		Female	
	Number	%	Number	%
0	585	95.1	568	96.6
1	11	1.8	5	0.9
2	5	0.8	2	0.3
3	4	0.7	4	0.7
4	2	0.3	0	
5	1	0.2	3	0.5
6	1	0.2	0	
8	0		1	0.2
9	0		1	0.2
10	0		1	0.2
11	1	0.2	0	
14	2	0.3	0	
15	2	0.3	1	0.2
19	0		1	0.2
20	0		1	0.2
66	1	0.2	0	

1987 through December 1988, a 21 consecutive month period. There were only three subadult males and two subadult females infected. Each subadult male had a single larva while one subadult female had 10 and the other 25 larvae. There were 30 adult male deer mice infected with a total if 187 larvae and 20 adult female deer mice infected with a total of 117 larvae. Infected male mice accounted for 4.9% of the male mouse population caught during the 21 mo period. Infected female mice accounted for 3.4% of the total female population caught during the same time period. There was no statistically significant difference between the prevalence rates or the number of larvae per adult mouse based upon the sex of the mouse.

The distribution of larvae within the adult deer mouse population shows an overdispersion pattern. (Table 5). Thus out of 1,203 adult mice examined over the 21 mo period 4.2% were infected. Within the infected group 46% (23) accounted for 10% (3) of the strobilocerci found. Alternatively, 16% (8) of the adult mice accounted for 59% (178) of the total strobilocerci found. The mean parasite intensity was 0.25, while the variance was 5.59.

There were only 5 (1%) of the 484 subadult deer mice caught during the April 1987 to December 1988 period infected. The small subadult sample size precluded statistical analysis.

DISCUSSION

Definitive hosts for *T. taeniaeformis* include wild and domestic members of the Felidae and Canidae families (Schmidt, 1986; Abduladze, 1964) which are infected with mature tapeworms in the digestive tract. Definitive hosts may harbor more than a single adult *T. taeniaeformis* and the more frequent their association with a particular geographic area and/or the greater their abundance, the greater is the opportunity for large numbers of ova to accumulate in the habitat (Huffman and Jones, 1962; Custer and Pence, 1981). The availability of viable ova to the susceptible deer mouse population is an important aspect in producing a consistent infection rate. *Taenia* ova are known to be highly resistant to certain environmental conditions. For example, Lucker (1960) reported that *Taenia saginata* ova could survive 2 wk at 24 F (−4 C) in water and a "few" ova survived 11 weeks at this temperature. Mackie and Parnell (1967) also demonstrated that *Taenia hydatigena*, *T. ovis* and *T. pisiformis* were resistant to the penetration of a wide variety of chemical compounds including 50% formalin. Laws (1968) has emphasized that desiccation appears to be a rapidly lethal insult to *Taenia* ova. However, he pointed out that exposure of the ova to temperatures of 38 C and 50 C for several hours or to sunlight or to artificial ultraviolet light had little effect as long as the ova were moist. A great reduction in the expected number of cysts occurred in the livers of rabbits exposed to *T. pisiformis* ova when the ova had been previously held for 24 hr at 20 C under a variety of relative humidities lower than 25%. Treatment of the ova at 60% relative humidity caused little reduction in infectivity.

Although bounded on both sides by open water, our study area is not conducive to holding moisture. The vegetation on this man-made, treeless area is composed primarily of relatively sparse mixed weeds growing on a permeable, diatomaceous earth substrate. Thus, in addition to seepage, this area is susceptible to evaporation of water as a result of exposure to solar radiation and wind current.

The terminal six proglottides of mature *T. taeniaeformis* contain mature, immature and developing ova (Huffman and Jones, 1962). New gravid proglottides continue to develop throughout the life of the adult tapeworm which may live as long as the definitive host. Ova from gravid proglottides in the feces of these mammalian predators may be liberated following defecation via proglottid motility or as a result of maceration of the proglottid due to desiccation in the external environment (Gon-

nert et al., 1968). Dispersal of viable ova from fecal material may also be enhanced via action of wind and surface water drainage.

The intermediate stage (strobilocercus) of *T. taeniaeformis* occurs in the liver of various rodent species. These intermediate hosts become infected by ingesting the ova containing the hexacanth embryo. After hatching, the embryo burrows through the mucosa of the small intestine, enters the portal circulation and is carried thereby to the liver. Encysted embryos (about 2 mm in diameter) are clearly visible in the liver within 10 days of infection and the larval form is fully developed within 40 days (Singh and Rao, 1967). Ingestion of an infected intermediate host by a definitive host completes the life cycle of this tapeworm, thus exhibiting a well-defined example of predator-prey relationship within the host community.

The mechanisms involved in the life-cycle of a parasite transmitted between predator and a prey species may depend upon a wide variety of factors including relative population densities, differential sex- or age-related infection potentials, annual and/or seasonal changes in host and parasite abundance, potential effects on host reproduction and survival, seasonal vulnerability of parasite ova to climatic conditions, etc. The results of our study suggest several possible relationships between parameters of the parasite and the host populations.

Since encysted *T. taeniaeformis* strobilocerci are clearly visible in the liver within 10 days of infection, the significant difference in *T. taeniaeformis* prevalence levels in the livers of subadult compared to adult *P. maniculatus* is not an artefact of differential detection. Lewis and Twigg (1972) reported a significant age-related prevalence rate of helminths (including *T. taeniaeformis*) in an "ecological equivalent" (Montgomery, 1989) of *P. maniculatus*, the adult old world wood mice (*Apodemus sylvaticus*) (17% in adults and 5% in subadults). These authors believed that the relatively limited foraging activities of the subadults were the most important factor resulting in differential age-related infection levels. There are, however, other possibilities.

Investigations by Lloyd and Soulsby (1978) have shown that neonatal mice fed purified colostrum IgA or injected intraduodenally with intestinal IgA from *T. taeniaeformis*-immune donors were protected against infection. They also found that neonates of immune mothers, but suckled by non-immune mothers, were protected to at least 21 days of age against infection with *T. taeniaeformis*. This suggests that transplacentally transferred IgA or IgG may also confer immunity to neonatal mice during their first few weeks of life (Lloyd and Soulsby, 1974). Passively-acquired immunity among rodents may have species-specific implications. Investigations on rats suggest that although transplacental transfer of IgA may not passively confer immunity to *T. taeniaeformis*, neonates can acquire such immunity via IgA from the colostrum of immune rats (Musoke et al., 1975).

Another mechanism, apparently discrete from infection-acquired immunity, has been reported to reduce the rate of infection by *T. taeniaeformis* in older animals. Greenfield (1942) showed that rats less than 25 days as well as those older than 60 days of age were resistant to infection. A similar bimodal pattern of resistance to infection also occurs in mice. Singh and Rao (1971), citing evidence reported by Schultz and Andreev, suggest that mice younger than 25 days and those older than 30 days of age are less susceptible to infection than are those between 25 and 30 days of age. That older mice are relatively resistant to infection also has been substantiated by Singh and Rao (1971) who were unable to infect adult albino mice with ova of *T. taeniaeformis*.

Thus, it appear that rodents may possess a period of high susceptibility for infection by *T. taeniaeformis* which occurs between 25–30 days of age in mice and 25–60 days

of age in rats. Because of this, the low level of infection found in subadult *P. maniculatus* during our study might be the result of capture of animals during the period of passive immunity or prior to their exposure to the entire period of highest susceptibility to *T. taeniaeformis* eggs. Differential survival favoring *T. taeniaeformis*-infected subadults does not seem a plausible explanation for the higher prevalence among adults. The animals in our "adult" age classification were older than 30 days and thus had been exposed to *T. taeniaeformis* eggs throughout the entire period of highest susceptibility to infection before being captured. Further, although adult rodents may possess age-related resistance, they are not entirely immune to infection by *T. taeniaeformis* (Greenfield, 1942; Singh and Rao, 1967). Thus, it seems likely that mice could continue to ingest ova periodically throughout their life and that some of these would develop into cysts.

Lewis and Twigg (1972) report higher *T. taeniaeformis* prevalence among male *A. sylvaticus* (15 of 86, 17.4%) than among females (four of 51, 7.8%). They suggest that the differential infection is the result of sex-related differences in hormones and/or in foraging activity. In contrast, although there are pronounced ecological similarities between *A. sylvaticus* and *P. maniculatus*, we found no significant sex-related differences in *T. taeniaeformis* infection levels among either the subadult or the adult components of our *P. maniculatus* population. The 4,501 mice examined during the 4-year duration of our study should have been sufficient to detect sex-related differences in *T. taeniaeformis* infections if they occur in this *P. maniculatus* population. It is also possible that the sex-related infection levels reported by Lewis and Twigg (1972) in the *A. sylvaticus* population are a result of insufficient sample size since they examined only 51 female and 86 male mice.

The *P. maniculatus* population examined during our study has the potential to breed throughout the year but with the greatest amount occurring during the summer months (Table 3). Because of this, we examined the possibility that *T. taeniaeformis* infection might curtail host reproduction on a seasonal as well as on an annual basis. The results demonstrate that *T. taeniaeformis* infection did not, either seasonally or between years, significantly impair the ability of adult deer mice to become pregnant. The possibility remains that infection might curtail reproductive success via other avenues such as a reduction in number of implantations, birth weight, number of neonates, quantity/quality of milk, etc. It is also possible that infection might impair the mother's ability to rear the young as reported by Weatherly (1971) for Swiss mice infected with *Trichinella spiralis*. It is also possible that the number of larvae per mouse is so low that the physiological reserve of the liver is able to overcome any damage produced by the parasites' presence.

Relative densities (number of mice captured per 100 trap-nights) of the host population during the four years of this study provided an ample opportunity to determine seasonal and annual relationships between host density and parasite abundance. For example, the average seasonal host density during 1985 was high (84) and relatively stable ranging from 98 during spring to 60 during the fall. In contrast, the average seasonal density during 1988 was only 29, although seasonal levels were also relatively stable (ranging from 40 during spring to 15 during the summer). The greatest variation between seasons during a given year occurred during 1987 when host densities ranged from 94 in winter to 11 during summer (Table 4).

In spite of pronounced fluctuations in the abundance of the host populations, there was no significant difference in annual *T. taeniaeformis* infection levels in either the adult or subadult populations during any of the four years of this study. This suggests that the annual numerical relationship between susceptible hosts and the density of viable ova within the habitat

remained relatively constant. Seasonally stable infection levels of *T. taeniaeformis* in old world wood mice, *A. sylvaticus*, have been documented by Langley and Fairley (1982). Further, the single seasonally significant difference in infection rates documented during our study occurred among the adult *P. maniculatus* during the combined winter–spring seasons of 1985. However, there was no significant seasonal difference in infection rates of adults during 1986 to 1988 and no significant seasonal differences in infection rates occurred in subadult mice over the entire study.

The distribution of the intermediate stage (Strobilocerci) shows an overdispersion pattern (Anderson, 1978; Anderson and Gordon, 1982; Crofton, 1971a, b). That is, a very few of the hosts contained most of the parasites. Under these circumstances the calculated variance is considerably larger than the average parasite burden per host. As shown in Table 5, mean parasite intensity was 0.25, while the variance was 5.59. This type of distribution can be expected to develop from several factors including (1) a random series of exposures with chances of infection differing at each exposure, (2) a nonrandom distribution of the infective stages, (3) the infection decreasing the chance of further infections, (4) or variation in the hosts' individual resistance to infection or their ability to kill the parasite once infected (Crofton, 1971a, b; Anderson and Gordon, 1982). As was noted above, the characteristics of this host-parasite association contribute to each of the factors listed above. Because proglottides containing large numbers of ova may remain intact, there is initially at least a clumped distribution of the infective stages to the intermediate host. This nonrandom distribution can result in numerous ova being ingested at a single time if a proglottid is eaten. At the same time these proglottides may be randomly found by the mice, since we are not aware of evidence demonstrating that deer mice actively search out or are attracted to feces and tapeworm proglottides. There is evidence to suggest that mice may have passive immunity and age resistance to infection with strobilocerci. The time periods through which these two factors operate could create a narrow (5 day) window of maximum susceptibility. These factors would have the effect of creating a variably susceptible mouse population within the habitat at any given point in time. Finally the climatic effects upon this habitat are conducive to desiccation, an insult that the ova are not resistant to. This could also result in a nonrandom distribution of infective ova since only those ova in areas of cover would survive for any length of time.

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