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INFLUENCE OF HABITAT MODIFICATION ON THE INTESTINAL HELMINTH COMMUNITY ECOLOGY OF COTTONTAIL RABBIT POPULATIONS

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ABSTRACT: The influence of five brush management treatments using the herbicides tebuthiuron and triclopyr, with or without prescribed burning, on the intestinal helminth community of cottontail rabbits (*Sylvilagus floridanus*) was studied in 1987 on the Cross Timbers Experimental Range in Payne County, Oklahoma (USA). Six helminth species were found (*Dermatoxys veligera*, *Trichostrongylus calcaratus*, *Passalurus nonanulatus*, *Wellcomia longejector*, *Taenia pisiformis* cystercercus, and *Mosgovoyia pectinata americana*) in 102 rabbits (88 adult and 14 juveniles) collected over two seasons (winter and summer). Prevalence of *M. pectinata americana* in cottontail rabbits was significantly greater in untreated control pastures than herbicide treated pastures in winter, while prevalence of *T. pisiformis* was significantly greater in burned than unburned pastures. Abundances of helminth species in the intestinal tract of cottontail rabbits were unaffected by brush treatments. *Mosgovoyia pectinata americana* abundance demonstrated a highly significant increase from winter to summer; conversely, abundance of all oxyurid pinworms combined (*D. veligera*, *P. nonanulatus*, *W. longejector*) was significantly higher in winter than summer. Helminth community dynamics were significantly influenced by season, but were unaffected by brush treatments. Habitat modification could have influenced cestode transmission by altering the ecology of invertebrate and vertebrate hosts.

Key words: Cottontail rabbit, *Sylvilagus floridanus*, helminth community, herbicides, triclopyr, tebuthiuron, prescribed burning, brush management, *Mosgovoyia pectinata americana*, *Taenia pisiformis*, Oxyuridae, Trichostrongylidae.

INTRODUCTION

Parasite communities in the eastern cottontail rabbit (*Sylvilagus floridanus*) show considerable geographical variation in species richness and abundance (Ward, 1934; Morgan and Waller, 1940; Smith, 1940; Moore and Moore, 1947; Franklin et al., 1966; Stringer et al., 1969; Novelsky and Dyer, 1970; Andrews et al., 1980; Strohlein and Christensen, 1983). Previous studies indicate that geographical variation in helminth community dynamics is associated with extrinsic habitat factors which change across geographic regions (Custer and Pence, 1981; Pence et al., 1983; Corn et al., 1985). For example, parasite populations in the cotton rat (*Sigmodon hispidus*) have been shown to differ between mesic and xeric habitats (Mollhagen, 1978; Kinsella, 1974). Jacobson et al. (1978) reported differences in abundances of helminths in cottontail rabbit populations from southeast and southwest Virginia associated with a variety of habitat factors.

Habitat factors vary not only across the geographic range of a host species but temporarily within the habitat of a resident population. Natural, progressive, successional changes as well as man-induced habitat alterations can change a variety of habitat factors in a local area. Induced changes of extrinsic habitat factors such as these could easily alter host, parasite community, and habitat interrelationships. However, only a few studies have actually examined the effects of habitat alterations on host-parasite community relationships. Issac (1963) reported that liver fluke and lungworm infections of blacktailed deer (*Odocoileus hemionus*) were curtailed by wildfires in Oregon. Similarly, Bendell (1974) found a strong relationship between elapsed time after a wildfire and internal and external parasitism of blue grouse (*Dendragapus obscurus*). Spratt (1987) determined that differences found in the helminth communities of eight species of small mammals exposed to wildfire in New South Wales, Australia were associated with ecological strategies of the hosts.

Cottontail rabbits are ubiquitous herbivore components of the cross timbers ecosystem in central Oklahoma (USA). To reduce woody plant cover and increase herbaceous understory production herbicides and prescribed burning are recommended techniques for improving grazing potential in the cross timbers. These brush management strategies usually result in dramatic alterations in both habitat structure and composition (Scifres, 1980). The objective of our study was to examine the impact of these brush management strategies in the cross timbers on parasite communities of the cottontail rabbit by analyzing distribution, abundance, intensity, prevalence, and species richness of intestinal helminths.

MATERIALS AND METHODS

Study area

Our study area was conducted on the Cross Timbers Experimental Range (CTER), which is located approximately 11 km west of Stillwater, Oklahoma (36°02′40″ to 36°04′20″N, 97°09′30″ to 97°11′39″W). The CTER is a 648-ha research area originally composed of blackjack oak (*Quercus marilandica*)-post oak (*Q. stellata*) and eastern redcedar (*Juniperus virginiana*) upland forest intermixed with tallgrass prairie (Ewing et al., 1984). The CTER includes 20 32.4-ha (0.42 × 0.83 km) fenced experimental pastures, representing four replications of four brush management treatments, using combinations of herbicide and annual prescribed burning applications and an untreated-control. This provides a 2 × 2 factorial design of four replications of five treatments (Fig. 1). The experimental treatments include: (1) tebuthiuron (N-[5-(1,1-dimethyl-ethyl)-1,3,4-thiadiazol-2 yl]-N,N′-dimethylurea), a soil applied herbicide (Elanco Products Co., Division of Eli Lilly and Co., Indianapolis, Indiana 46285, USA), applied aerially at 2.0 kg per ha in March 1983; (2) tebuthiuron applied as in treatment (1) with annual prescribed burning beginning April 1985; (3) triclopyr ([(3,5,6-trichloro-2-pyridinyl) oxy] acetic acid), a foliage applied herbicide (Dow Chemical Co., Midland, Michigan 48674, USA), applied aerially at 2.2 kg per ha in June 1983; (4) triclopyr applied as in treatment (3) with annual prescribed burning beginning in April 1985; and (5) an untreated control. No control was established for evaluating the effects of prescribed burning without herbicide treatment. All experimental pastures were moderately grazed by cattle during the spring and summer.

Herbicide-treated pastures produced more grasses and forbs compared to the untreated control pastures (Engle et al., 1987). Both herbicides killed a high proportion of the dominant overstory oak species, but woody understory species such as buckbrush (*Symphoricarpos orbiculatus*), elm (*Ulmus americana*) and chittamwood (*Bumelia lanuginosa*) were not reduced as much by triclopyr as by tebuthiuron (Stritzke et al., 1987). Competition by understory woody species reduced the production of herbaceous plants after the triclopyr treatment.

Data collection

Forest floor material (litter and mulch <1.5 m above the soil surface) was collected from each pasture within seven caged quadrats (50 × 50 cm) placed inside grazing exclosure cages randomly located within a permanent sampling location in each pasture. Samples, collected from mid-July through mid-August, were dried in a forced air oven at 70 C and weighed. Differences between treatments were determined by two-way analysis of variance.

An attempt was made to collect five cottontail rabbits from each of two replications for each treatment in winter (January) and summer (July) of 1987. Carcasses were necropsied within 24 hr of collection or frozen until necropsy could be performed. Thoracic, abdominal and pubic cavities were thoroughly searched for the presence of *T. pisiformis* larvae. Intestinal tracts were removed from the carcasses at necropsy and the entire tract was dissected laterally and examined grossly for tapeworms. Contents were then collected and stored in 70% ethanol for subsequent microscopic examination. Small intestinal contents were filtered through a 150 μm sieve (W. S. Tyler Co., Mentor, Ohio 44060, USA) and a 25% aliquot of the non-filterable material was examined. The combined cecal and large intestinal contents were sieved as above and a 10% aliquot was examined. Parasites were counted and stored in 70% ethanol. Nematodes were cleared with lactophenol and identified by microscopic examination. Tapeworms were fixed in alcohol-formalin-acetic acid (AFA) then stained with Delafields iron hematoxylin differential stain. Representative specimens of helminth species were deposited in the U.S. National Parasite Collection (Beltsville, Maryland 20705, USA; Accession Numbers 80495 to 80500).

Data analysis

Abundance, intensity and prevalence are defined by Margolis et al. (1982). Species richness is expressed as the number of helminth species. Host age was determined using a combination of reproductive status and body weight. Cottontail rabbits ≥800 g body weight and reproductively active individuals between 650 and 799 g were considered adults. The parasite community of a small sample of juveniles (n = 13) collected in the summer differed from adults; hence, only adult cottontail rabbit (n = 88) abundance data were analyzed for main effects of treatment, season and sex. Overdispersion is defined by Bliss and Fisher (1953) and is used to describe the frequency distributions of common (≥25% prevalence) species of intestinal helminths where a small number of host individuals harbor many helminth individuals and many of the hosts harbor few or no individuals of a particular helminth species (Waid et al., 1985; Corn et al., 1985). Overdispersion was indicated when the variance for a particular species was significantly ($P \leq 0.050$) larger than the mean abundance using a chi-square distribution (χ^2, $[s^2/\bar{x}] \times$ df). The degree of overdispersion was measured by the negative binomial parameter k (Bliss and Fisher, 1953) which is an inverse measure of the degree of overdispersion. Differences in overdispersion (k) among brush treatments and seasons were evaluated by factorial anlaysis of variance using Anscombe's transform (common k estimate), $\text{Log}_{10}(x + 1/2k)$, of abundance observations (Bliss and Owen, 1958). Overdispersed helminth abundances for the 88 sample data set were independently rank transformed (Conover and Iman, 1981; PROC RANK, Statistical Analysis Systems, 1985, SAS Institute, Raleigh, North Carolina 27512, USA) for each common parasite species prior to data analysis as a method to analyze non-normally distributed data (Conover and Iman, 1981; Waid et al., 1985).

The main and interactive effects of treatment, season and sex were examined with a factorial analysis of variance and multivariate analysis of variance (MANOVA) for the ranked abundances of recovered helminth species (PROC GLM, SAS). Oxyurid (*Dermatoxys veligera, Wellcomia longejector, Passalurus nonanulatus*) abundances were combined and analyzed as one dependent variable. Specific contrasts were utilized to compare variation in abundance data within brush treatment categories (burned herbicide-treated versus unburned, tebuthiuron versus triclopyr, control versus brush treated). Protected multiple comparisons (LSD) were used when analysis of variance rejected the null hypothesis that brush treatment categories were similar. Prevalence data was subjected to chi-square analysis to determine homogeneity between seasons and brush treatment. Biological significance was set at $P \leq 0.1$ for data analyses. Copies of the raw and rank transformed data are available upon request from R. L. Lochmiller.

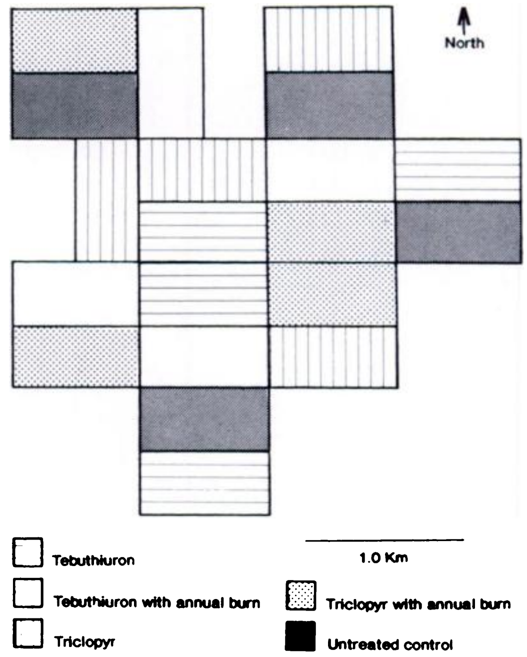

FIGURE 1. Map of the Cross Timbers Experimental Range, consisting of 20 experimental pastures representing four replications of four treatments and an untreated control.

RESULTS

Forest floor material

Forest floor material (Fig. 2) represented accumulations of dead vegetation at ground level. Leaf litter was the primary component of forest floor material in untreated pastures. Forest floor material differed ($P < 0.001$) between the control and brush treatments. No differences ($P > 0.1$) in these accumulations were found between triclopyr and tebuthiuron-treated

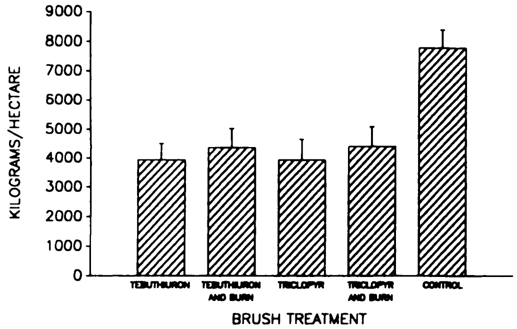

FIGURE 2. Amount of forest floor material on five experimental brush treatments (herbicide and prescribed burning) at the Cross Timbers Experimental Range, Payne County, Oklahoma.

pastures. Untreated control pastures had about 60% more material accumulated on the forest floor than the brush treatments.

Helminth fauna

Four species of intestinal nematodes (*D. veligera*, *P. nonanulatus*, *T. calaratus*, and *W. longejector*) and two species of cestodes (*T. pisiformis* and *M. pectinata americana*) were recovered from 102 cottontail rabbits (88 adults, including 44 male and 44 female; 14 juveniles). Most helminth species were common, occurring in all experimental treatments in both winter and summer. *Welcomia longejector* occurred in only two animals, both collected from the same pasture; a tebuthiuron treatment subjected to annual burning. Species richness showed no relationship with experimental treatment.

Mean abundances of *T. pisiformis* and *M. pectinata americana* were significantly ($P < 0.1$) different between adults and juveniles (Table 1). There were no age-related differences in mean abundances for *D. veligera*, *T. calcaratus*, and *P. nonanulatus*.

Helminth prevalence

Prevalence (Table 2) of *D. veligera* infection in cottontail rabbits differed significantly ($P < 0.005$) between seasons, with lower prevalences in winter (6%) than summer (58%). There were no seasonal differences ($P > 0.1$) in prevalence of *T. calcaratus*, *P. nonanulatus*, *T. pisiformis*, *M. pectinata*, and *W. longejector*. There was also no difference ($P > 0.1$) in prevalence between seasons for all species of oxyurids (*P. nonanulatus*, *D. veligera*, *W. longejector*) combined.

Prevalence of *M. pectinata americana* and *T. pisiformis* infections were significantly affected by experimental brush treatments (Table 2). Prevalence of *M. pectinata americana* was higher ($P < 0.01$) on untreated controls (100%) than herbicide treated pastures (53%). There were no differences ($P > 0.1$) in prevalence of *M. pectinata americana* infections between burned and unburned treatments or tebuthiuron and triclopyr treatments. Prevalence of *T. pisiformis* infection was higher ($P < 0.05$) on burned (93%) than on unburned (65%) treatments. No differences ($P > 0.1$) existed in prevalence of *T. pisiformis* between untreated controls and herbicide treatments or tebuthiuron and triclopyr treatments. Over-

TABLE 1. Mean abundances (standard error) of intestinal helminth parasites of adult ($n = 88$) and juvenile ($n = 14$) cottontail rabbits collected from the Cross Timbers Experimental Range, Payne County, Oklahoma, in winter and summer 1987.

Parasites	Adult	Juvenile
Taenia pisiformis[a]	9.3 (2.2)	2.3 (1.4)
Trichostrongylus calcaratus	262.1 (35.6)	259.7 (91.9)
Mosgovoyia pectinata[b]	2.2 (0.4)	2.9 (0.8)
Passalurus nonanulatus	281.8 (116.6)	404.3 (398.9)
Dermatoxys veligera	7.7 (3.0)	2.9 (2.9)

[a] Significantly different ($P \leq 0.05$).
[b] Significantly different ($P \leq 0.1$).

TABLE 2. Prevalence of infection (number infected/number examined) by intestinal helminth parasites found in adult cottontail rabbits ($n = 88$) collected from five experimental brush treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma, in winter and summer 1987.

	Brush treatment									
	Tebuthiuron		Tebuthiuron with burn		Triclopyr		Triclopyr with burn		Control	
Parasites	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Nematoda										
Trichostrongylus calcaratus	9/9	10/10	9/9	11/11	7/8	9/9	4/5	9/10	7/7	10/10
Passalurus nonanulatus	4/9	1/10	3/9	2/11	3/8	2/9	1/5	5/10	3/7	4/10
Dermatoxys veligera	2/9	0/10	5/9	2/11	5/8	0/9	0/5	0/10	2/7	1/10
Wellcomia longejector	0/9	0/10	2/9	0/11	0/8	0/9	0/5	0/10	0/7	0/10
Oxyurids (total)	6/9	1/10	7/9	4/11	6/8	2/9	1/5	5/10	4/7	5/10
Cestoda										
Taenia pisiformis[a]	6/9	9/10	8/9	10/11	5/8	6/9	5/5	8/10	4/7	9/10
Mosgovoyia pectinata[b]	8/9	5/10	7/9	7/11	8/8	7/9	4/5	3/10	5/7	10/10

[a] Significant ($P \leq 0.01$) brush treatment effects for winter specimens.
[b] Significant ($P \leq 0.05$) brush treatment effects for summer specimens.

all prevalences of *D. veligera* (19%), *W. longejector* (2%), *P. nonanulatus* (32%), and *T. calcaratus* (97%) were not affected by brush treatment. Prevalence of all species of oxyurids combined was 47%.

Helminth abundance and intensity

Mean rank abundance and intensity data for helminths recovered from our study showed no significant differences ($P > 0.1$) between male and female cottontail rabbits (Table 3, 4). However, mean rank abundances of *T. calcaratus, M. pectinata americana*, and all species of oxyurids combined showed significant season by sex interactions. *Trichostrongylus calcaratus* ($P < 0.06$) and *M. pectinata* ($P < 0.1$) infections during summer were higher among females than males, while the reverse was true in winter. Conversely, in all species of oxyurids combined, abundances were higher ($P < 0.097$) among females in winter and higher among males in summer.

TABLE 3. Mean abundances (standard error) of intestinal helminth parasites of adult male ($n = 44$) and female ($n = 44$) cottontail rabbits collected from the Cross Timbers Experimental Range, Payne County, Oklahoma, in winter and summer 1987.

	Summer		Winter	
Parasites	Male ($n = 21$)	Female ($n = 17$)	Male ($n = 23$)	Female ($n = 27$)
Nematoda				
Trichostrongylus calcaratus	117.7 (56.2)	164.5 (59.8)	405.9 (58.8)	313.2 (64.7)
Passalurus nonanulatus	453.3 (414.1)	251.2 (193.1)	185.7 (99.3)	249.6 (151.5)
Dermatoxys veligera	23.8 (11.6)	8.2 (3.5)	1.3 (1.0)	0.4 (0.4)
Wellcomia longejector	4.8 (4.8)	2.9 (2.9)	0	0
Oxyurids (total)	481.9 (417.8)	262.4 (196.1)	187.0 (99.2)	250.0 (151.4)
Cestoda				
Mosgovoyia pectinata	3.1 (1.1)	5.3 (1.4)	1.0 (0.2)	0.6 (0.1)
Taenia pisiformis	6.4 (1.8)	22.7 (10.5)	5.7 (2.0)	6.1 (1.3)

TABLE 4. F values for main effects and interactions generated by MANOVA and factorial ANOVA for five experimental brush treatments, season and host sex across the 88-sample data set of rank abundances for the intestinal helminths in cottontail rabbits collected from the Cross Timbers Experimental Range, Payne County, Oklahoma, winter and summer 1987.

	MANOVA	Factorial ANOVA			
		Trichostrongylus calcaratus	*Taenia pisiformis*	*Mosgovoyia pectinata*	Oxyurids
Treatment	0.85	0.23	0.57	0.53	0.54
Season	13.84***	24.21***	0.34	16.84***	4.34**
Sex	0.18	0.02	0.62	1.26	0.08
Treatment/Season	1.18	0.44	1.31	0.59	2.05*
Treatment/Sex	0.46	0.27	0.35	0.51	1.25
Season/Sex	2.35*	3.67*	1.52	2.73*	0.05
Treatment/Season/Sex	0.95	0.47	0.97	1.06	0.25

* $P \leq 0.1$.
** $P \leq 0.05$.
*** $P \leq 0.001$.

Except for *T. pisiformis*, abundances for all helminths in our study differed significantly between seasons (Table 4, 5). Mean rank abundances were lower for *T. calcaratus* ($P < 0.001$), and higher for *M. pectinata americana* ($P < 0.001$) and all species of oxyurids combined ($P < 0.041$) in summer than winter. Mean intensities were also higher for *M. pectinata americana* ($P < 0.001$) and *T. pisiformis* ($P < 0.048$) in summer than winter. Mean intensities for all other helminths did not differ ($P > 0.1$) between seasons. Mean rank abundances and intensities for all helminths recovered showed no significant relationship ($P > 0.1$) to brush treatment.

Multivariate analysis of variance indicated that mean rank abundances of species within helminth communities were significantly ($P < 0.001$) influenced by season, with a significant ($P < 0.064$) season by sex interaction. However, no significant differences ($P > 0.1$) were apparent between host sexes or among brush treatments (Table 4).

Helminth distribution

All helminth species recovered with the exception of *M. pectinata,* had variances significantly ($P < 0.05$) larger than respective mean abundances across all treatments and seasons (Table 6), indicating an overdispersed distribution (Bliss and Fisher, 1953). However, variances of *M. pectinata americana* were not significantly ($P > 0.05$) larger than respective mean abundances in winter, but showed significant ($P < 0.05$) overdispersion in summer. A low range of *M. pectinata* infection (0 to 4), with only one rabbit having an intensity of four cestodes, was responsible for low variances within winter samples. Analysis of variance for common k estimates (Table 7) revealed significant seasonal effects for the distribution of *T. calcaratus* ($P < 0.001$), *M. pectinata americana* ($P < 0.004$), and all species of oxyurids combined ($P < 0.017$); however, no significant differences in helminth distribution (k values) were detected among brush treatments. *Trichostrongylus pisiformis* distribution was not affected ($P > 0.1$) by season or brush treatment.

DISCUSSION

Effects of habitat modification

Spring burning is a common practice in the tallgrass prairie and cross timbers because it removes dead herbage and litter, which often improves the diet quality of herbivores (Allen et al., 1976; Grelen and Epps, 1967; McGinty et al., 1983) and induces succession of plant communities to dominance by tallgrasses (Engle, 1987). Prescribed burning on the CTER occurred in late March and early April, when helminth infective stages and invertebrate intermediate hosts should have been abundant and conditions for transmission were ideal. However, herbicides effected the greater change in vegetation by reducing oak (*Quercus* sp.) and other hardwoods in the overstory and increasing herbaceous understory production (Engle et al., 1987). Plant communities of both burned and unburned herbicide-treated pastures have undergone retrogression since 1984 when herbicides were first applied (Stritzke et al., 1987).

Helminth fauna new to Oklahoma

Mosgovoyia pectinata americana, *W. longejector*, and *D. veligera* are reported for the first time in eastern cottontail rabbits from Oklahoma. *Mosgovoyia pectinata americana* (formerly *Cittotaenia pectinata*; Arnold, 1938) has been recovered from the small intestine of cottontail rabbits from a variety of locations (Erickson, 1947; Novelsky and Dyer, 1970). *Welcomia longejector* was first described by Hannum (1943) from lagomorphs and rodents in Arizona. *Dermatoxys veligera*, a common oxyurid of cottontail rabbits, has been found in Kansas (Franklin et al., 1966) and other locations in the United States (Cheatum, 1943; LeDune, 1933; Llewellyn and Handley, 1945; Jacobson et al., 1978; Moore and Moore, 1947; Novelsky and Dyer,

TABLE 5. Mean abundance and intensity data (standard error) for intestinal helminths collected from 88 adult cottontail rabbits during winter and summer 1987 from five experimental brush treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma.

Brush treatment		*Trichostrongylus calcaratus*		*Mosgovoyia pectinata*	
		Summer	Winter	Summer	Winter
Tebuthiuron	A[a]	90.2 (23.1)	300.0 (66.7)	3.0 (1.3)	0.6 (19.5)
	I[b]	90.2 (23.1)	300.0 (66.7)	3.4 (1.4)	1.2 (0.2)
Tebuthiuron and burn	A	188.9 (129.8)	403.3 (70.3)	4.6 (2.5)	1.0 (0.4)
	I	188.9 (129.8)	403.3 (70.3)	5.9 (3.0)	1.6 (0.4)
Triclopyr	A	96.5 (34.8)	354.2 (107.2)	5.9 (2.4)	0.8 (0.2)
	I	110.3 (36.8)	354.2 (107.2)	5.9 (2.4)	1.0 (0.0)
Triclopyr and burn	A	272.0 (201.9)	355.2 (113.1)	4.4 (2.3)	0.3 (0.2)
	I	340.0 (245.5)	394.7 (118.5)	5.5 (2.6)	1.0 (0.0)
Control	A	89.1 (22.9)	361.6 (142.1)	2.7 (1.0)	1.4 (0.2)
	I	89.1 (22.9)	361.6 (142.1)	3.8 (1.0)	1.4 (0.2)

[a] A, abundance.
[b] I, intensity.

1970; Stringer et al., 1969; Rozycki, 1941; Strohlein and Christensen, 1983). With the exception of *W. longejector*, these helminth species are probably common components of the helminth community of cottontail rabbits in Oklahoma, and their delayed documentation is due to limited helminth research on wildlife species in Oklahoma (Ward, 1934; Smith, 1940).

Cestode parasitism

Cottontail rabbits serve as definitive hosts for *M. pectinata americana* and intermediate hosts for *T. pisiformis*. Orbatid mites are common intermediate hosts for anoplocephaline cestodes such as *M. pectinata americana* (Stunkard, 1941). *Taenia pisiformis* exists as a larval cystercercus in the intermediate host, developing into an adult tapeworm in canines. Overall prevalence of *M. pectinata americana* was considerably higher than the 5% reported in cottontail rabbits from Minnesota (Erickson, 1947) and 7% from North Dakota (Novelsky and Dyer, 1970). Unlike *Cittotaenia* (=*Mosgovoyia*) sp. infections in cottontail rabbits from Virginia (Jacobson et al., 1978) and Kentucky (Strohlein and Christensen, 1983), seasonal differences in prevalence of *M. pectinata* were not evident in our study.

Observed differences in the prevalence of *M. pectinata* infections among experimental brush treatments could have been a reflection of intermediate host availability. Prevalence of *M. pectinata americana* in cottontail rabbits has been shown to be related to the availability of soil dwelling orbatid mites. Mitchell (1979) reported that orbatid mite survival is highly temperature dependent and species diversity is limited by specific microhabitat factors such as soil depth, moisture, preferred food resources, and degree of microbial decomposition. Seastedt (1984) reported a linear correlation between microarthropod population numbers, to include orbatid mites, and the amount of leaf litter on the forest floor. Defoliation by herbicides has been shown to increase midday soil temperatures (Santillo et al., 1989). Burning (Heyward and Tissot, 1936; Pearse, 1943) as well as herbicide applications (Guerra et al., 1982) can reduce acarine soil mite abundance. Greater accumulations of organic matter on the forest floor and an overstory canopy providing more optimal abiotic conditions (temperature, humidity) could have contributed to higher abundances of infected orbatid mites in untreated control pastures compared to herbicide treated pastures on the CTER.

TABLE 5. Continued.

Taenia pisiformis		*Passalurus nonanulatus*		Oxyurids (total)	
Summer	Winter	Summer	Winter	Summer	Winter
35.0 (19.5)	5.4 (1.5)	78.9 (58.2)	37.0 (37.0)	82.2 (57.6)	37.0 (37.0)
52.5 (27.1)	6.0 (1.5)	177.5 (120.2)	370.0 (0.0)	123.3 (83.4)	370.0 (0.0)
10.1 (2.1)	5.1 (1.3)	1,060.0 (961.4)	149.1 (119.5)	1,092.2 (970.0)	150.9 (118.9)
11.4 (1.9)	5.6 (1.4)	3,180.0 (2,778.7)	820.0 (480.0)	1,404.3 (124.0)	415.0 (305.0)
6.5 (2.7)	4.3 (2.4)	418.8 (404.6)	290.0 (211.5)	472.5 (405.6)	290.0 (211.5)
10.4 (3.1)	6.5 (3.3)	1,116.7 (1,066.8)	1,305.0 (535.0)	630.0 (536.0)	1,305.0 (535.0)
7.4 (2.1)	6.5 (2.7)	2.0 (2.0)	341.0 (313.5)	2.0 (2.0)	31.4 (20.9)
7.4 (2.1)	8.1 (3.2)	10.0 (0.0)	682.0 (619.8)	10.0 (0.0)	55.0 (33.0)
3.6 (2.1)	8.2 (1.9)	25.7 (20.9)	298.0 (274.0)	341.0 (313.5)	300.0 (273.7)
6.3 (3.0)	9.1 (1.9)	60.0 (45.1)	745.0 (672.3)	682.0 (619.8)	600.0 (540.6)

Taenia pisiformis prevalence was similar to historical surveys in Oklahoma by Ward (1934) and Smith (1940). This larval cystercercus was found primarily in the thoracic cavity, mesenteric tissue, and along the pubic symphysis region. *Taenia pisiformis* gains access into the rabbit as a result of ingesting infective eggs while foraging. The higher prevalence of *T. pisiformis* in cottontail populations from burned experimental pastures was unexpected. The CTER supports an abundant population of coyotes (*Canis latrans*) and it is probable that increased contact of cottontail rabbits with coyotes took place on pastures which were burned. Increased forage value as a result of prescribed burning (Grelen and Epps, 1967) could have increased cottontail rabbit densities, prompting a higher degree of coyote utilization of these habitats. A sparsity of brush and overstory canopies may also have promoted higher coyote utilization of burned pastures. Increased deposition of infective eggs in the habitat would be expected with increased coyote utilization.

Jacobson et al. (1978) reported seasonal influences on *Cittotaenia* (=*Mosgovoyia*) sp. abundances in cottontail rabbits from Virginia which were similar to ours. Although cestodes were prominant in cottontail populations in both summer and winter on the CTER, Strohlein and Christensen (1983) found *M. pectinata* in cottontail rabbits only in spring and winter. Differences between seasons and host sex in our study were also consistent with previous surveys of cottontail rabbits in Virginia (Jacobson et al., 1978).

Nematode parasitism

Prevalence of *T. calcaratus* infection in cottontail populations on the CTER was higher than previously reported surveys in Oklahoma (Ward, 1934; Smith, 1940) and other southeastern localities (Andrews et al., 1980). Abundance estimates of *T. calcaratus* were higher than previous studies in Oklahoma (Smith, 1940). Physiological stresses incurred during lactation and pregnancy could have contributed to the observed season and host sex differences in *T. calcaratus* infections of cottontail rabbits on the CTER. Dunsmore (1966) reported similar seasonal effects for *Trichostrongylus retortaeformis* in European rabbits (*Oryctolagus cuniculus*) where infections increased 10 fold in female hosts during the breeding season. The increased abundance of *T. calcaratus* observed from summer to winter on the CTER was inconsistent with previous surveys of cotton-

TABLE 6. Determination of overdispersion and measure of degree of aggregation of helminth parasites in cottontail rabbits collected from five brush management treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma, based on the frequency distribution of individual parasites recovered from 88 hosts in winter and summer 1987. Values of k were derived from Bliss and Fisher, 1953.

	Brush treatment									
	Tebuthiuron		Tebuthiuron with burn		Triclopyr		Triclopyr with burn		Control	
Parasites	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Nematoda										
Trichostrongylus calcaratus	1.70*[a]	2.04	0.24*	3.01	0.97*	0.99	0.36*	0.99*	2.22*	0.65*
Passalurus nonanulatus	0.21*	0.10*	0.14*	0.14*	0.13*	0.21*	0.22*	0.12*	0.22*	0.12*
Dermatoxys veligera	0.24*	—	0.84*	0.13*	0.47*	—	—	—	0.27*	0.11*
Wellcomia longejector	—	—	0.23*	—	—	—	—	—	—	—
Oxyurids	0.23*	0.10*	0.14*	0.15*	0.17*	0.21*	0.22*	0.12*	0.33*	0.12*
Cestoda										
Taenia pisiformis	0.36*	1.83	3.58*	1.83	0.85*	0.40*	3.68*	0.62*	0.50*	2.35*
Mosgovoyia pectinata	0.75*	3.24	0.42*	2.50	0.87*	1.04*	0.86*	1.50	1.91*	1.73

[a] Values of k.

* Variance is significantly ($P \leq 0.05$) larger than the mean.

tail rabbits in the southeastern United States (Andrews et al., 1980; Jacobson et al., 1978).

Oxyurids, like *T. calcaratus*, have a direct life cycle, without intermediate hosts, where infective eggs are transmitted by ingestion (Soulsby, 1982). Prevalence of infection was comparable to the combination of *P. ambiguus* and *D. veligera* in southeastern United States (Andrews et al., 1980), lower than the same combination from cottontail rabbits in Alabama (Moore and Moore, 1947), and higher than *P. ambiguus* and *P. nonanulatus* in Minnesota (Erickson, 1947). Observed seasonal differences in oxyurid infections were probably a reflection of both altered intrinsic variables (host behavior, physiological condition) and optimal environmental conditions for survival of infective eggs in spring and summer. Low k values demonstrated that oxyurid pinworms infected relatively few cottontail rabbits with high intensity.

The helminth community

Except for *T. pisiformis*, helminth distribution in cottontail rabbits inhabiting the CTER was influenced most by season. A combination of intrinsic and extrinsic variables may have contributed to seasonal shifts in the frequency distribution pattern of helminth communities. For example, infections by *M. pectinata* in winter were primarily with mature adult tapeworms where range and intensity of infections were low (probably established during the previous summer or fall). Conversely, some infections in summer were dominated by immature tapeworms (<1.0 cm long) and intensities were high. The shift from a normal to an overdispersed distribution for *M. pectinata* could be a result of seasonal differences in orbatid mite distribution as well as host intrinsic variables, including differences between sexes (reproductive-immunologic interactions) as suggested by a significant season by sex interaction, and changes in habitat use (behavior).

Our study was not designed to address the mechanisms by which shifts in frequency distribution of helminths occur. However, these data indicate that extrinsic variables such as brush treatment can be as important as intrinsic variables in influencing the population dynamics of certain helminth species (such as prevalence of cestodes) of the cottontail rabbit. Other natural successional or managment-induced modifications of the habitat could potentially alter host–parasite community relationships as well. Further research efforts may ultimately allow us to accurately predict how various habitat modifications will influence host–parasite relationships. Management of parasitic diseases could become more routine with the availability of such predictive capabilities.

TABLE 7. F values for main effects generated by ANOVA for Anscomb's Transform of frequency distribution data (Common k; Bliss and Owen, 1958) for helminth species in cottontail rabbits collected from five experimental brush treatments at the Cross Timbers Experimental Range, Payne County, Oklahoma, winter and summer 1987.

Main effects	Parasites			
	Trichostrongylus calcaratus	*Taenia pisiformis*	*Mosgovoyia pectinata*	Oxyurids
Treatment	0.27	1.47	1.37	0.66
Season	16.95**	0.02	8.92**	6.02*

* $P \leq 0.05$.
** $P \leq 0.01$.

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