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INFLUENCE OF HABITAT MODIFICATION ON THE COMMUNITY OF GASTROINTESTINAL HELMINTHS OF COTTON RATS

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ABSTRACT: Dynamics of communities of gastrointestinal helminths of cotton rats (*Sigmodon hispidus*) were monitored in response to five experimental brush management treatments using herbicide applications with and without prescribed burning on the Cross Timbers Experimental Range in Payne County, Oklahoma (USA). A total of 113 adult cotton rats (68 male and 45 female) was collected from experimental pastures in winter and summer 1986 resulting in the recovery of five species of helminths: *Longistriata adunca, Syphacia sigmodontis, Strongyloides* sp., *Protospirura muris,* and *Raillietina* sp. Prevalences of *Raillietina* sp. and *S. sigmodontis* were greater on control than herbicide-treated pastures. Prevalence and abundance of *Raillietina* sp. and prevalence of *S. sigmodontis* were significantly lower on annually burned, herbicide-treated pastures compared to unburned herbicide-treated pastures. Triclopyr-treated pastures had greater abundances of *L. adunca* and lower abundances of *Raillietina* sp. than those treated with tebuthiuron. Abundances of *L. adunca* also decreased from winter to summer on annually burned, herbicide-treated pastures while increasing on other pastures. Distribution of all helminths was overdispersed, but distribution of *L. adunca* showed a significant brush treatment by season interaction as a result of greater overdispersion in summer than winter for cotton rats inhabiting brush-treated pastures. Our results indicate that man-induced habitat modifications can alter host-parasite relationships in the community.

Key words: Cotton rat, *Sigmodon hispidus,* habitat modification, parasitism, helminth community ecology, brush management, tebuthiuron, triclopyr, prescribed burning.

INTRODUCTION

A great amount of geographical variation exists in the composition of helminth communities harbored by a particular host population (Pence et al., 1983; Andrews et al., 1980). Most of this geographic variation is thought to be due to differences in extrinsic habitat variables, including both abiotic and biotic components (Kinsella, 1974; Mollhagen, 1978; Martin and Huffman, 1980). However, habitat factors vary not only across the geographic range of a host species but also across time within the habitat of a resident population. Man-induced and natural successional changes commonly occur, potentially altering a variety of abiotic and biotic characteristics of the habitat.

Few studies have examined the influences of local habitat changes on the dynamics of helminth communities of resident host populations. Issac (1963) and Bendell (1974) reported changes in helminth communities of black-tailed deer (*Odocoileus hemionus columbianus*) and blue grouse (*Dendragopus obscurus*), respectively, following wildfires. Similarly, Seip and Bunnell (1985) noted reductions in *Protostrongylus* sp. in Stone's sheep (*Ovis dalli stonei*) utilizing annually burned alpine ranges. We found differences in the prevalence of cestodes in cottontail rabbit (*Sylvilagus floridanus*) populations as a result of herbicide and fire-induced habitat modifications (Boggs et al., 1990). We also observed influences on abundances and frequency distributions of certain nematode populations (Boggs et al., 1990).

Cotton rats (*Sigmodon hispidus*) are important small mammal components of the cross timbers ecosystem in central Oklahoma (USA). Herbicide applications, alone or combined with prescribed burning, are commonly used techniques for improving livestock grazing potential on brush-infested rangelands in the cross timbers region. These brush management strategies typically result in dramatic alterations in both habitat structure and composition (Scifres, 1980). We used the cotton rat as an animal model for evaluating the potential impact of these brush management strategies on helminth community dynamics in the cross timbers of Oklahoma. Specifically, we examined the influences of herbicide and herbicide with fire applications on the distribution, abundance, prevalence, and species richness of gastrointestinal helminths of the cotton rat.

MATERIALS AND METHODS

Study area

This study was conducted on the Cross Timbers Experimental Range (CTER) which is located approximately 11 km west of Stillwater, Oklahoma (36°2′40″ to 36°4′20″N, 97°9′30″ to 97°11′39″W). The CTER is a 648-ha research area composed of blackjack oak (*Quercus marilandica*)-post oak (*Q. stellata*) savannas intermixed with eastern redcedar (*Juniperus virginiana*) and prairies of short and tall grasses (Ewing et al., 1984). The CTER includes 20 32.4-ha (0.42 km × 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 (Boggs et al., 1990). This provided an experimental design with four replications of five treatments. The five experimental treatments included: (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 2.2 kg per ha in March 1983; (2) tebuthiuron applied (as with treatment 1) with annual prescribed burning in April, beginning in 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 with treatment 3 with annual prescribed burning in 1985; (5) untreated control. Prescribed burning was not evaluated as a separate treatment because it does not represent a viable brush management option on cross timbers rangeland without herbicide application (Stritzke et al., 1987). All experimental pastures were moderately grazed by cattle throughout spring and summer.

Herbicide-treated pastures produced more grasses and forbs compared to 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 with understory woody species reduced the production of herbaceous plants after triclopyr treatment (Engle et al., 1987).

Data collection

Cotton rats were collected from the CTER from July to September 1986 (summer) and December 1986 to January 1987 (winter). Due to extremely low densities of cotton rats on experimental control pastures in winter on the CTER, we expanded our collections of animals to include untreated cross timbers rangeland on adjacent (within 2.5 km) research lands to serve as controls. Cotton rats were sampled by removal snap-trapping using a randomly placed 8 × 8 transect grid with 15 m spacing between trap stations within each pasture. Snap traps were baited with a peanut butter-rolled oats mixture and apples for three consecutive days. Cotton rats were frozen immediately after collection and later necropsied and eviscerated as time allowed. Eviscerated intestinal contents were filtered with a 150 micron sieve (W. S. Tyler Co., Mentor, Ohio 44060, USA) and a 10 or 50% aliquot (depending upon volume of contents) of nonfilterable material was retained for enumeration of nematodes. Total recovery of tapeworms and stomach worms was attempted by gross examination of the viscera and gut contents.

Nematodes were stored in 70% ethanol and examined in lactophenol wetmounts. Cestodes were fixed in acetic acid–formalin ethyl alcohol, stained in acetocarmine and mounted in permount (Fisher Scientific Co., Fair Lawn, New Jersey 07410, USA). Representative samples of helminths recovered from this study have been deposited in the U.S. National Parasite Collection (Beltsville, Maryland 20705, USA; Accession numbers 80566 to 80570).

Data analysis

The terms abundance, intensity and prevalence were used as defined by Margolis et al. (1982). Only adult cotton rats (n = 113) were used for helminth recovery and all available hosts were examined, resulting in a data set of 113 specimens. No statistical analysis for *Protospirura muris* abundance data was performed due to low prevalence.

Overdispersion was defined by Bliss and Fisher (1953) and is used to describe the frequency distributions of common (>15% prevalence) helminth species where a small number of host individuals harbor many individual parasites of a particular helminth species (Waid et al., 1985; Corn et al., 1985). Overdispersion is indicated when helminth frequency distributions revealed a variance significantly larger ($P \leq 0.050$) than the mean abundance using a chi-square distribution. 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 then evaluated by analysis of variance using Anscombe's transform, $\text{Log}_{10}(x + \frac{1}{2}k)$, of abundance data (Bliss and Owen, 1958). Overdispersed helminth abundances for the 113 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). Specific contrasts were used to compare variation in abundance data within brush treatment categories (burned herbicide-treated versus unburned herbicide-treated, tebuthiuron-treated versus triclopyr-treated, and control versus herbicide-treated). Protected multiple comparisons (LSD) were used when significant differences ($P < 0.100$) were detected by analysis of variance. Prevalence was subjected to chi-square analysis for determination of heterogeneity between brush treatments and seasons. Statistical significance was set at $P \leq 0.100$. Copies of the raw and rank transformed data are available upon request from Robert L. Lochmiller.

RESULTS

Species richness

Four nematodes (*Longistriata adunca*, *Strongyloides* sp., *P. muris*, *Syphacia sigmodontis*) and one cestode (*Raillietina* sp.) were recovered from 113 (68 male and 45 female) cotton rats (Table 1). *Raillietina* sp., *L. adunca*, and *Strongyloides* sp. were recovered from cotton rat populations on all brush treatments. *Protospirura muris* was found only in cotton rats collected from annually burned tebuthiuron and control pastures. *Syphacia sigmodontis* was not recovered from cotton rats on annually burned triclopyr-treated pastures.

Prevalence

Prevalence of *S. sigmodontis* and *Raillietina* sp. in cotton rat populations were significantly ($P < 0.050$) influenced by experimental brush treatments (Table 1). Prevalence of *S. sigmodontis* infection was greater ($P < 0.050$) in populations from control (46%) than brush-treated (13%) pastures. Prevalence of *Raillietina* sp. infections was greater ($P < 0.050$) on control (53.8%) than brush-treated (26%) pastures and greater ($P < 0.005$) on tebuthiuron (34%) than triclopyr-treated (18.9%) pastures. Cotton rat populations from unburned herbicide treatments (37% and 19%) also had greater ($P < 0.05$) prevalences of *Raillietina* sp. and *S. sigmodontis* infections than those collected from burned herbicide treatments (15% and 6%, respectively). Prevalence of *Strongyloides* sp. in cotton rats was greater ($P < 0.100$) on brush-treated (30%) than control (8%) pastures.

Prevalence of *P. muris* was high in populations of cotton rats collected from control pastures in winter (63%); only one cotton rat from brush-treated habitat (annually burned tebuthiuron) was infected with *P. muris* (Table 1). Prevalences of other helminths were not significantly ($P > 0.100$) affected by season.

Helminth abundance and intensity

Mean rank abundances of *Raillietina* sp. were ($P < 0.001$) affected by brush treatment. Cotton rats collected from unburned herbicide treatments had greater ($P < 0.002$) abundances of *Raillietina* sp. compared to burned herbicide treatments (Tables 2 and 3). Mean rank abundances of *Raillietina* sp. were also greater ($P < 0.043$) in cotton rats from tebuthiuron-treated than triclopyr-treated pastures. Abundances of *Raillietina* sp. were not different

TABLE 1. Prevalence of infection (number infected/number examined) by intestinal helminth parasites recovered from 113 adult cotton rats (*Sigmodon hispidus*) collected from five experimental brush treatments at the Cross Timbers Experimental Range, Payne County, Oklahoma, during summer and winter 1986.

Parasites	Brush treatment										
	Tebuthiuron		Tebuthiuron with burn		Triclopyr		Triclopyr with burn		Control		
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Total[a]
Longistriata adunca	10/12	10/10	11/12	11/13	14/15	14/15	11/11	12/12	5/5	7/8	93
Strongyloides sp.	5/12	3/10	1/12	6/13	5/15	4/15	3/11	3/12	0/5	1/8	27
Syphacia sigmodontis	3/12	0/10	3/12	0/13	4/15	3/15	0/11	0/12	1/5	5/8	17
Protospirura muris	0/12	0/10	1/12	0/13	0/15	0/15	0/11	0/12	0/5	5/8	5
Raillietina sp.	7/12	6/10	1/12	2/13	4/15	2/15	3/11	1/12	2/5	5/8	29

[a] Expressed as %.

TABLE 2. Mean abundance and intensity data (standard error) for intestinal helminths recovered from 113 adult cotton rats (*Sigmodon hispidus*) collected from five experimental brush treatments at the Cross Timbers Experimental Range, Payne County, Oklahoma, summer and winter 1986.

Brush treatment		*Longistriata adunca*		*Strongyloides* sp.		*Syphacia sigmodontis*		*Raillietina* sp.	
		Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Tebuthiuron	A[a]	234.4 (92.2)	113.4 (32.4)	5.0 (3.3)	4.8 (3.5)	40.5 (24.3)	0	2.5 (1.1)	1.3 (0.6)
	I[b]	281.3 (104.9)	113.4 (32.4)	12.0 (7.2)	16.0 (9.5)	162.0 (55.8)	0	4.3 (1.6)	2.2 (0.8)
Tebuthiuron with burn	A	160.4 (57.1)	181.1 (55.8)	0.3 (0.3)	5.2 (2.4)	337.2 (333.4)	0	0.1 (0.1)	0.2 (0.1)
	I	175.0 (60.4)	214.0 (60.9)	4.0 (0)	11.3 (4.1)	1,348.7 (1,327.7)	0	1.0 (0)	1.0 (0)
Triclopyr	A	388.9 (139.8)	166.5 (35.5)	7.6 (3.3)	2.6 (1.6)	543.3 (425.1)	3.9 (2.7)	0.3 (0.1)	0.2 (0.1)
	I	416.7 (147.1)	178.4 (35.9)	22.8 (5.1)	9.8 (4.4)	2,037.5 (1,465.5)	19.3 (9.8)	1.0 (0)	1.5 (0.5)
Triclopyr with burn	A	190.9 (68.8)	335.5 (54.5)	8.2 (4.4)	1.2 (0.8)	0	0	0.7 (0.4)	0.8 (0.8)
	I	190.9 (68.8)	335.5 (54.5)	30.0 (5.8)	4.7 (2.7)	0	0	2.7 (1.2)	1.0 (0)
Control	A	542.8 (124.7)	22.5 (10.4)	0	0.3 (0.3)	7.2 (7.2)	354.0 (280.6)	0.4 (0.2)	1.0 (0.5)
	I	542.8 (124.7)	25.7 (11.4)	0	2.0 (0)	36.0 (0)	566.4 (436.4)	1.0 (0)	1.6 (0.6)

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

($P > 0.100$) between control and brush-treated pastures. Abundance of *Raillietina* sp. was also influenced by host sex, being greater ($P < 0.039$) in male than female cotton rats. Season had no influence ($P > 0.100$) on the abundance of *Raillietina* sp. in cotton rats.

Mean rank abundance of *S. sigmodontis* differed significantly ($P < 0.006$) among brush treatments as well (Tables 2 and 3). Abundances of *S. sigmodontis* were greater ($P < 0.012$) for cotton rats obtained from control pastures compared to brush-treated pastures. A treatment by season interaction ($P < 0.056$) indicated that abundance of *S. sigmodontis* in cotton rats from herbicide-treated pastures decreased from winter to summer, while the reverse was true for cotton rats from control pastures. There were no significant ($P > 0.100$) differences in abundances of *S. sigmodontis* between seasons or host sexes.

Triclopyr-treated pastures supported cotton rat populations with significantly greater ($P < 0.016$) abundances of *L. adunca* than tebuthiuron-treated pastures (Tables 2 and 3). A significant ($P < 0.001$) treatment by season interaction was indicated as abundances of *L. adunca* from winter to summer decreased in cotton rat populations from annually burned herbicide treatments while increasing for those from unburned herbicide treatments. No significant ($P > 0.100$) differences in abundances of *L. adunca* were found between host sexes or seasons.

Abundance of *Strongyloides* sp. was not significantly ($P > 0.100$) affected by brush treatment, season, or host sex (Table 2 and 3). Cotton rat populations from brush-treated pastures had significantly ($P < 0.100$) higher mean abundances of *Strongyloides* sp. than those from control pastures. Mean abundance of *P. muris* infection was 2.6 ± 1.0 worms per host in control pastures in winter. Only one cotton rat was found infected with *P. muris* (collected from an annually burned tebuthiuron pasture) in summer.

Helminth distribution

All parasites indicated a high ($k \leq 0.10$) degree of overdispersion throughout the year across all treatments. Analysis of distribution (k) data was only performed for *Strongyloides* sp. and *L. adunca*; data on the distribution of other helminth species were not suitable for statistical analysis (Table 4). Distribution patterns of *Strongyloides* sp. were not significantly ($P > 0.100$) affected by host sex, season, or brush treatment. However, distribution of *Strongyloides* sp. did show a significant ($P < 0.004$) treatment by season interaction. A greater degree of overdispersion of *Strongyloides* sp. occurred in cotton rat populations from triclopyr-treated pastures in winter than summer, while the reverse was true for cotton rats from tebuthiuron-treated pastures. Degree of overdispersion of *L. adunca* was greater ($P < 0.051$) in cotton rats from tebuthiuron-treated than triclopyr-treated pastures. Distribution of *L. adunca* showed a significant ($P < 0.006$) treatment by season interaction; overdispersion in summer was greater for cotton rats from herbicide-treated pastures than controls. No significant ($P > 0.100$) differences were found in the distribution of *L. adunca* due to host sex, or season.

Helminth community

Multivariate analysis of variance (Table 3) indicated that the overall helminth community (*L. adunca, S. sigmodontis, Strongyloides* sp., *Raillietina* sp.) was strongly influenced by brush treatment ($P < 0.001$) with a significant treatment by season interaction ($P < 0.001$). The helminth community was not significantly ($P > 0.100$) influenced by season or host sex. Specific contrasts between brush treatment categories indicated that helminth communities harbored by cotton rat populations differed in mean rank abundance between control and treated ($P < 0.020$), burned and unburned herbicide treatments ($P < 0.012$), and tebuthiuron and triclopyr ($P < 0.025$) pastures.

TABLE 3. F values for main effects and interactions generated by MANOVA and factorial ANOVA for five experimental brush treatments, season and host sex across the 113-sample data set of rank abundances for the intestinal helminths in cotton rats collected from the Cross Timbers Experimental Range, Payne County, Oklahoma, winter and summer 1986.

		Factorial ANOVA			
Effect	MANOVA	*Longistriata adunca*	*Strongyloides* sp.	*Syphacia sigmodontis*	*Raillietina* sp.
Treatment	2.95***	1.96	0.92	3.87***	6.61***
Season	1.45	1.83	0.08	1.56	0.32
Sex	1.41	1.30	0.08	0.02	4.41**
Treatment/Season	2.93***	7.13***	1.33	2.40*	0.87
Treatment/Sex	1.46	2.27*	0.96	0.75	1.18
Season/Sex	0.40	0.16	1.50	0.81	0.01
Treatment/Season/Sex	0.46	0.16	0.36	0.32	0.83

* $P \leq 0.100$.
** $P \leq 0.050$.
*** $P \leq 0.010$.

DISCUSSION

Effects of brush treatment

Tebuthiuron and triclopyr treatments significantly altered the vegetative community of the CTER by decreasing woody overstory and increasing understory productivity over that of typical cross timbers habitat (Engle et al., 1987; Stritzke et al., 1987). Prescribed burning on herbicide-treated pastures removes litter and increases forage quality while favoring fire-tolerant vegetation (Ewing and Engle, 1988). Fleharty and Mares (1973) found that *S. hispidus* of central Kansas preferred vegetative communities composed of weeds and dense grasses which provided ample cover and food. Brush treatments used on the CTER should have provided abundant cover and preferred food for cotton rats. However, untreated-control pastures representing typical cross timbers habitat, probably provided inadequate amounts of cover and food, resulting in extremely low cotton rat population densities. Relative population densities of cotton rats on the CTER were significantly greater on brush-treated than control pastures, greater on tebuthiuron than triclopyr, and greater on burned herbicide-treated than unburned herbicide-treated pastures (McMurry, 1989).

Helminth fauna new to Oklahoma

Syphacia sigmodontis, Strongyloides sp., *L. adunca*, and *P. muris* are reported for the first time in cotton rats from Oklahoma. *Syphacia sigmodontis* was collected from the cecum and large intestine and has been reported from Texas (Martin and Huffman, 1980; Mollhagen, 1978) and Florida (Kinsella, 1974). *Strongyloides* sp. is believed to be *Strongyloides sigmodontis* (Melvin and Chandler, 1950), a common parasite of cotton rats. It was not possible to harvest filariform larvae from cotton rats collected in our study, so positive identification of species was not possible. *Strongyloides sigmodontis* has been identified from cotton rats in Texas (Martin and Huffman, 1980; Scott and Blynn, 1952) and Florida (Kinsella, 1974). *Protospirura muris* (syn. *Mastophorus muris*) is a spirurid stomach worm of rodents including cotton rats in Florida (Kinsella, 1974), Texas (Mollhagen, 1978), and Virginia (Seidenberg et al., 1974). *Longistriata adunca* (syn. *Hassalstrongylus aduncus*), a trichostrongylid nematode inhabiting the small intestine, was the most widely distributed and prevalent helminth of our study, and it has been reported from Texas (Melvin and Chandler, 1950; Scott and Blynn, 1952), North Carolina (Coggins and McDaniel, 1975), Virginia (Sei-

TABLE 4. Determination of overdispersion and measure of aggregation (k) for the distribution frequencies of helminth species recovered from 113 adult cotton rats (*Sigmodon hispidus*) collected from five experimental brush treatments at the Cross Timbers Experimental Range, summer and winter, 1986. k values derived from Bliss and Fisher (1953).

Parasites	Brush treatment										
	Tebuthiuron		Tebuthiuron with burn		Triclopyr		Triclopyr with burn		Control		
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Overall
Longistriata adunca	0.54*	1.24*	0.66*	0.81*	0.52*	1.48*	0.70*	3.19*	3.82*	0.60*	0.61*
Strongyloides sp.	0.20*	0.20*	0.11*	0.39*	0.38*	0.20*	0.32*	0.19*	NE[a]	0.25*	0.18*
Syphacia sigmodontis	0.23*	NE	0.08*	NE	0.11*	0.15*	NE	NE	0.20*	0.20*	0.03*
Raillietina sp.	0.50*	0.74*	NE	NE	NE	NE	0.35*	NE	NE	NE	0.19*

* Variance is significantly (χ^2; $P < 0.050$) larger than the mean abundance.

[a] Not estimatable.

denberg et al., 1974), and Florida (Kinsella, 1974).

Heteroxenous helminths

Raillietina sp. was the only cestode recovered from cotton rats on the CTER and we narrowed identification to either *R. bakeri* or *R. sigmodontis*. Prevalence of *Raillietina* sp. recorded from a previous study in Texas (Mollhagen, 1974) was similar to ours; however, higher prevalences have been reported in Florida (Kinsella, 1974) and North Carolina (Coggins and McDaniel, 1975). Abundance of *Raillietina* sp. in our study was considerably less than that reported from Virginia (Seidenberg et al., 1974) but was similar to that reported from Texas (Mollhagen, 1978). The stomach worm, *P. muris*, was found less frequently in cotton rat populations from our study area than in previous surveys from Texas (Mollhagen, 1978), Florida (Kinsella, 1974), and Virginia (Seidenberg et al., 1974).

Observed differences in abundance and prevalence of *Raillietina* sp. and *P. muris* among cotton rat populations on the CTER probably reflected availability of intermediate hosts. Insects from the orders Diptera (house flies), Coleoptera (meal worms and cockroaches), and Hymenoptera (ants) can harbor *Raillietina* sp. infections (Horsfall, 1938; Ackert, 1922), while intermediate hosts of spirurids (*P. muris*) include orthopterans and coleopterans (Yamaguti, 1961). In general, arthropods have been found to respond negatively to burning and herbicide application (Guerra et al., 1982; Seastedt, 1984; Warren et al., 1987). Seastedt (1984) found that prescribed burning in Kansas reduced microarthropod numbers. Santillo et al. (1989) reported decreased abundances of coleopteran, dipteran, orthopteran, and hymenopteran insects on forest clear cuts treated with glyphosphate herbicide in Maine. These negative effects on insect hosts of *P. muris* and *Raillietina* sp. could have contributed to the low prevalence of these helminths in cotton rat populations from brush-treated pastures. This relationship also is consistent with previous research about the effects of brush treatment on tapeworm (*Mosgovoyia pectinata*) parasitism of cottontail rabbits from the same study area (Boggs et al., 1990). Host sex effects on *Raillietina* sp. have been previously documented (Coggins and McDaniel, 1975) and are consistent with our findings.

Monoxenous helminths

Longistriata adunca was the most frequently encountered and abundant helminth recovered from cotton rats in our study. Prevalence and abundance of this intestinal nematode reported from Virginia (Seidenberg et al., 1974) and North Carolina (Coggins and McDaniel, 1975) were much lower than ours. Prevalence and abundance of *L. adunca* in cotton rats from Florida were similar to our estimates, and appear to be directly related to soil moisture (Kinsella, 1974). Our abundance data suggested that triclopyr-treated pastures provided better conditions for *L. adunca* infection than tebuthiuron-treated pastures. The woody understory of triclopyr-treated pastures probably provides more shade than the open grassland habitats of tebuthiuron-treated pastures, possibly resulting in a more optimal microclimate (i.e., temperature, soil moisture) for the survival of trichostrongyle larvae (Soulsby, 1982). Differences in movement and feeding habits of cotton rats in response to differing plant communities across treatments could have influenced *L. adunca* infections as well.

Both prevalences and abundances of *Strongyloides* sp. in cotton rats on the CTER were higher than previous surveys from upland habitats in Florida (Kinsella, 1974). The higher degree of *Strongyloides* sp. infection among cotton rat populations from brush-treated pastures could have been attributable to higher host densities found in the brush-treated pastures or alteration of the normal *Strongyloides* life cycle. Filariform larvae of *Strongyloides sigmodontis* infect cotton rats by penetrating the skin (Melvin and Chandler, 1950). All species of *Strongyloides* are heterogenetic, producing alternating free-living and parasitic generations (Soulsby, 1982). Primvati (1958) found that variation in soil pH, temperature, and food abundance altered normal heterogonic cycling, resulting in development of infective filariform larvae from parasitic female adults. Microclimate changes created by burning (Ewing and Engle, 1988) and herbicide application (Santillo et al., 1989) may have been responsible for a high proportion of parasitic generations on brush-treated pastures.

Prevalence and abundance of *S. sigmodontis* infection was higher in our study than from previously reported surveys in upland habitats of west Texas (Mollhagen, 1978) and central Texas (Martin and Huffman, 1980). Responses of *S. sigmodontis* infections to prescribed burning on herbicide treatments were similar to those of *Raillietina* sp. Both the direct effect of fire on deposited eggs and herbicide-induced modifications of the microclimate, as a result of litter and vegetation structural changes, were probably the primary factors in the habitat (Bendell, 1974; Issac, 1963; Seip and Bunnell, 1985) influencing infection of cotton rats.

Helminth community responses

Season and brush treatment were the most important extrinsic factors determining the degree of gastrointestinal helminth distribution in cotton rat populations on the CTER. This is consistent with previous studies on the ecology of parasitic helminths of various wildlife which determined that extrinsic variables such as season and habitat are important in determining dispersion patterns. Pence and Windberg (1984) found that the impact of these extrinsic variables influenced the intestinal helminth community in coyotes (*Canis latrans*). Waid et al. (1985) found seasonal influences to be more important than the intrinsic influence of host condition in determining overdispersion of intestinal helminths of white-tailed deer (*Odocoileus virginianus*). Corn et al. (1985) reported seasonal influences were important in the distribution of *Physocephalus sexalatus* in collared peccaries (*Tayassu tajacu*) collected from Texas. Boggs et al. (1990) also found that seasonal influence was the most important extrinsic factor regulating the distribution of the helminth community in cottontail rabbits.

Observed variation in helminth community dynamics in cotton rats across our brush treatments is consistent with previous studies comparing helminth communities across differing habitat types. Kinsella (1974) found that trematodes of cotton rats were absent in freshwater marshes and upland areas but were present in saltwater environments of Florida. He also found that *Raillietina* sp. was the dominant cestode in cotton rats from upland habitats while *Monoecocestus sigmodontis* (not found on the CTER) was the dominant cestode in saltwater and freshwater marshes. Martin and Huffman (1980) suggested that habitats similar in vegetation composition support similar helminth communities in the cotton rat. Microclimate has been shown to vary with vegetative manipulation (Ewing and Engle, 1988; Santillo et al., 1989) and could have been the most important factor responsible for helminth community variation among pastures on the CTER.

Results of our study suggest that habitat modification on the CTER altered several important factors (microclimate, host availability) which determine the "quality" of habitat for selected helminth species. The impact of these modified habitat "quality" factors on any particular helminth species is probably correlated with life cycle and mode of transmission of the respective helminth species as has been suggested by Pence and Windberg (1984).

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