EFFECTS OF HABITAT MODIFICATION ON THE PARASITE COMMUNITY ECOLOGY OF SMALL MAMMALS AND COTTONTAIL RABBITS OF OKLAHOMA

by

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DEDICATION

This work is dedicated to the memory of my grandfather

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PREFACE

The cross timbers region of Oklahoma covers an expansive area of central and eastern Oklahoma and supports a large part of the state's livestock production. Rugged topography and thick, woody brush hinder optimum forage quality and necessitate brush control withn which to maximize economic potential. Much research has been done to improve the effectiveness, effeciency and economic feasibilty of brush control practices such as prescribed burning and herbicide application. The feasibility of using combined applications of herbicide and prescribed burning to control brush and improve livestock grazing potential on cross timbers rangeland in Oklahoma is currently being explored at the Cross Timbers Experimantal Range in Payne County, Oklahoma. This 648 ha area of north-central Oklahoma is a mosaic of oak (Quercus sp.) woodlands; mixed grass prairies dominated by big bluestem (Andropogon gerardii), little bluestem (Schizachrium scoparium), and indian grass (Sorghastrum nutans); and shallow, sandy savannas invaded by eastern red cedar (Juniperus virginianus).

These woodlands, prairies and savannas provide suitable habitat for a community of small mammals (8 species) and cottontail rabbits (Sylvilagus floridanus) which coexist in this area with cattle. This community of vertebrates, as with any wildlife community, interacts with its parasitic component. This symbiotic interaction or relationship is termed host-parasite community ecology and is a poorly understood subject. This is especially true for those communities inhabiting the cross timbers region of Oklahoma.

Vegetative density, composition, height, canopy cover, and availability of forage to wildlife can be affected by burning and herbicide application, therefore influencing host-parasite relationships. The purpose of this study was to determine how applications of the herbicides triclopyr (3,5,6-trichloro-2-pyridinyloxyacetic acid) butoxyethyl ester and tebuthiuron (N-[5-(1,1 dimethyl ethyl)-1,3,4 thiadiazol-2-yl]-N,N' dimethylurea) with prescribed burning can influence host-parasite community ecology of small mammals and cottontail rabbits inhabiting the Cross Timbers Experimental Range.

This thesis is comprised of five manuscripts formatted for submission to the Journal of Wildlife Diseases. The manuscripts (chapters I, II, III, IV, and V) are complete as written and do not need supporting material.

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CHAPTER I

OBELISCOIDES CUNICULI PARASITISM IN COTTONTAIL RABBITS (*SYLVILAGUS FLORIDANUS*) IN RESPONSE TO HABITAT MODIFICATION IN CROSS TIMBERS OF OKLAHOMA

ABSTRACT: The influence of habitat modification on Obeliscoides cuniculi populations in cottontail rabbits (Sylvilagus floridanus) was examined from 1987 to 1988 in the cross timbers ecosystem of Oklahoma. Five experimental brush control treatments, using combinations of the herbicides tebuthiuron and triclopyr with or without prescribed burning, were replicated 4 times on 20 32.4 ha pastures. A total of 205 rabbits (25 juvenile and 180 adult) was collected with an overall prevalence of infection of 97%. Prevalence was not influenced by brush treatment, season, or year. Distribution of O. cuniculi populations within cottontail rabbits was significantly influenced by season, with a higher degree of overdispersion in winter. The influence of brush treatment on the degree of overdispersion was not clear, but seasonal variation was low on untreated control pastures. Abundance of O. cuniculi infections was significantly affected by brush treatment, season, and year of collection. Mean abundances were lower on annually burned triclopyr treatments than all other experimental pastures. Abundance of O. cuniculi in cottontail rabbits was higher in summer (58.8 ± 7.0) than winter (23.0 ± 4.4). Variations in the intensity of the prescribed burns and season were probably important factors that influenced O. cuniculi parasitism in cottontail rabbit populations.

Key words: Cottontail rabbit, Sylvilagus floridanus, brush management, Obeliscoides cuniculi, trichostrongylidae,

herbicides, prescribed burning, Tebuthiuron, Triclopyr.

INTRODUCTION

Parasitism in wildlife populations is strongly influenced by the type of habitat in which the host resides (Custer and Pence, 1981; Pence et al., 1983; Corn et al., 1985). Geographical variation in wildlife helminth communities appears to be associated in part with changes in selected habitat attributes. For example, Mollhagen (1978) suggested that helminth community composition in cotton rat (Sigmodon hispidus) populations in Texas was influenced by moisture characteristics of the habitat. Similarly, Kinsella (1974) reported significant differences in prevalence and abundance of nematode and cestode parasites among cotton rat populations in freshwater marshes, saltwater marshes, and relatively xeric upland habitats from north-central to south-central Florida. Jacobson et al. (1978) noted significant differences in abundances of nematode and cestode parasites of eastern cottontail rabbit (Sylvilagus floridanus) populations between southeast and southwest Virginia; however, these two areas differed markedly in altitude, topography, growing season duration, soil pH, and land management practices which made interpretation difficult.

Although previous studies demonstrate a strong relationship between parasite communities of a host and habitat attributes when compared across geographic regions, they provide little insight into host-parasite relationships following habitat alterations in a local area. Natural and man-induced successional changes are a common component of wildlife habitats. Intensive land-use and range/wildlife improvement practices are capable of drastic alterations of both the structure and composition of wildlife habitat, especially in the vegetative component. Management techniques such as prescribed burning and herbicide applications are routinely used to reverse succession across large areas of habitat with lasting effects. Changes in physical and biological attributes of habitat undoubtedly occur following intensive treatments such as these, and potentially can alter host-parasite community ecology.

Our understanding of effects of local habitat modification on host-parasite relationships is limited. Issac (1963) discovered that black-tailed deer (*Odocoileus hemonius columbianus*) diseases caused by liver flukes and lung worms were curtailed by the Tillamook burn of Oregon in 1933. Bendell (1974) found that although internal and external parasitism of blue grouse (*Dendragapus obscurus*) initially decreased following an intense wildfire, parasite species richness and frequency of infection increased 12 years later.

Obeliscoides cuniculi (Graybill, 1923) is a common trichostrongylid stomach worm of cottontail rabbits that is widely distributed in North America (Ward,1934; Morgan and

Waller, 1940; Moore and Moore, 1947; Franklin et al., 1966; Stringer et al., 1969; Andrews et al., 1980; Strohlein and Christensen, 1983). Several studies on O. cuniculi have examined their life history (Alicata, 1932), effects on rabbit nutritional physiology (Pace and Fransden, 1982), seasonal variation (Gibbs et al., 1977), and arrested development (Michel et al., 1975). However, only one study has investigated the distribution, abundance, and ecology of this trichostrongyle nematode within the Cross Timbers ecosystem of central Oklahoma (Ward,1934) where range improvement practices are commonly used. My objective was to determine if brush management strategies using combinations of fire and herbicides influence the distribution, abundance, or prevalence of O. cuniculi infections of cottontail rabbit populations in the Cross Timbers ecosystem of Oklahoma.

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. 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 tall grass prairie (Ewing et al., 1984). The CTER includes 20 32.4-ha (0.42 x 0.83 km) fenced experimental pastures, representing 4 replications of 4 brush management treatments, using combinations of herbicide and annual prescribed burning, and an untreated control. This provides a 2 x 2 factorial design consisting of 4 replications of 5 treatments (Appendix D). The experimental treatments included: (1) tebuthiuron (N-[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), 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), applied aerially at 2.2 kg per ha in June 1983; (4) Triclopyr applied (as with treatment #3) with annual prescribed burning in beginning in April 1985; and (5) untreated control. No treatments were burned in 1988. All experimental pastures were moderately grazed by cattle during the 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 by understory woody species reduced the production of herbaceous plants after the triclopyr treatment.

Data collection

A total of 205 cottontail rabbits was collected during winter (January) and summer (July) of 1987 and 1988. An attempt was made to collect 5 specimens from each of 2 replications for each treatment. Carcasses were necropsied within 24 hours of collection or frozen until necropsy could be performed. Stomach worms that were recovered from the gastric mucosa and food contents were counted and stored in 70% ethanol. O. cuniculi specimens were cleared with lactophenol and identified by microscopic examination. Representative specimens of O. cuniculi recovered from this study were deposited in the U. S. National Parasite Collection, Beltsville, Maryland 20705, U. S. A. (Accession No. 80494).

Data analysis

Abundance and prevalence were defined by Margolis et al. (1982). Host age was determined using a combination of reproductive status and body weight. Cottontail rabbits $\geq$ 800 g body weight and reproductively active individuals between 650 and 799 g were considered adults. Only abundance data for adult cottontail rabbits (n = 180) were used in data analyses for the main effects of treatment, season, year, and sex.

Overdispersion as defined by Bliss and Fisher (1953), has been used to describe frequency distributions of helminths in which a small number of host individuals harbor many helminth individuals and many hosts harbor little to no individuals of a particular helminth species (Waid et al., 1985; Corn et al., 1985). Overdispersion was indicated when helminth frequency distributions revealed a variance significantly larger ($\underline{P} \leq 0.05$) 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 rush treatments and seasons were then evaluated by analysis of variance using Anscombe's transform, $Log_{10}(x + 1/2k)$, of abundance data (Bliss and Owen, 1958). Overdispersed O. cuniculi abundances for the adult cottontail rabbits were independently rank transformed prior to data analysis as a method to analyze non-normally distributed data (Conover and Iman, 1981; Waid et al., 1985).

Main and interactive effects of treatment, season, and year on rank transformed abundances were examined with a factorial analysis of variance. Biological significance was set at $\underline{P} \leq 0.100$. Specific contrasts (1 df) were utilized to compare variation among treatment components (burned vs. unburned, untreated control vs. brush treatments, tebuthiuron vs. triclopyr). Protected multiple comparisons

(LSD) were used when significant (P ≤ 0.05) differences were detected by analysis of variance. The Statistical Analysis System (SAS) was used for all data analyses (SAS, 1985; SAS Institute, Raleigh, North Carolina). Copies of the raw and rank transformed data are available upon request from Robert L. Lochmiller.

RESULTS AND DISCUSSION

Prevalence

A total of 95 male (86 adult) and 110 female (94 adult) cottontail rabbits was collected from the CTER with an overall prevalence of 97% for O. cuniculi. Juvenile cottontail rabbits (n = 25) were not included in data analyses due to significant differences in O. cuniculi mean abundances (P ≤ 0.001) when compared to adults. Infection intensities ranged from 1 - 435 worms/host; only 5 uninfected rabbits were observed in winters of 1987 and 1988 (Table 1). Prevalence of O. cuniculi infections in my study was higher than other studies in Oklahoma and surrounding states. Ward (1934) and Smith (1940) reported prevalences of 47% and 0% in samples of 52 and 31 cottontail rabbits in Oklahoma, respectively. Franklin et al. (1966) had a prevalence of 16% in a sample of 138 cottontail rabbits from Kansas. O. cuniculi infections in our study were similar to surveys in the southeastern United States where prevalence approached 100% (Andrews et al., 1980; Jacobson et al., 1978; Moore and Moore, 1947). No differences in prevalence were found among cottontail rabbits from the brush treatments or controls.

Distribution and overdispersion

Variances were significantly larger than the mean number of *O. cuniculi* individuals/adult cottontail rabbit for all treatments in each season (Table 2), which was indicative of an overdispersed parasite distribution (Bliss and Fisher, 1953). Low k values (≤ 1.0) indicated a high degree of parasitic aggregation (Bliss and Fisher, 1953; Corn et al., 1985) within our host population, but there was no significant difference ($P \geq 0.100$) in k values due to brush treatment. Cottontail rabbit populations from herbicide-treated pastures showed a greater amount of variation in k values between seasons than those from untreated controls. Common k statistics from 1988 indicated differences ($P < 0.055$) between *O. cuniculi* overdispersion in control and brush-treated pastures. Degree of overdispersion was significantly greater ($P < 0.001$) in winter than summer for both years. The k value of 25 juvenile cottontail rabbits that were collected primarily in summer was 2.90.

Distribution of *O. cuniculi* infections in cottontail rabbit populations in the cross timbers supports previous studies that indicate seasonal changes foster overdispersion (Corn et al., 1985; Pence and Windberg, 1984). However, other factors such as habitat heterogeneity (Anderson, 1982) also could be important in overdispersion in O. cuniculi as indicated by differences in the seasonal variation of k values between treated and untreated pastures. Natural successional changes, vegetative composition, patchiness of treatments, and microclimates occurring on herbicide treated pastures could have contributed to these observed differences with untreated controls. Intrinsic host-related variables such as cottontail rabbit habitat use patterns also may be factors that contribute to overdispersion on my study area.

Abundance

Mean O. cuniculi abundances (Table 3) were significantly different between seasons ($P < 0.001$), treatments ($P < 0.057$), years ($P < 0.053$), and a significant ($P < 0.013$) brush treatment by year interaction occurred. Mean rank abundances were considerably higher in summer than winter for both years sampled. Mean abundance for O. cuniculi across all treatments was 58.8 ± 7.0 and 23.0 ± 4.4 worms/host (wph) for summer and winter, respectively. Mean abundance was higher in 1987 (42.8 ± 5.8 wph) than 1988 (34.0 ± 5.8 wph).

Mean rank abundances of O. cuniculi in cottontail rabbits collected in 1988 from annually burned treatments (41.1 ± 4.2 wph) were lower ($P < 0.040$) than those from unburned (48.0 ± 3.7 wph experimental treatments. Multiple comparisons among treatments showed triclopyr treatments subjected to annual prescribed burning had a mean rank abundance for O. cuniculi that was lower ($P < 0.050$) than the other four treatments. Abundances of O. cuniculi were not different ($P > 0.230$) between triclopyr and tebuthiuron-treated pastures in 1987 or 1988. There was no significant ($P > 0.150$) differences in abundances between control and treated pastures for 1987.

Seasonal differences between winter and summer O. cuniculi abundances in cottontail rabbits are well documented across the United States. Andrews et al. (1980) found that O. cuniculi abundances in cottontail rabbits collected in spring were 2 to 4 times greater than those in winter. Jacobson et al. (1978) reported similar results for cottontail rabbits from Virginia, and speculated that variable climate and host hormonal changes influenced O. cuniculi abundance. In our study, seasonal variation was more profound during 1988 than 1987 as demonstrated by a larger summer to winter ratio of mean rank abundance. This was probably due to a harsh winter in 1988, during which record snowfalls and ice storms were recorded. Winter of 1987 was mild and wet and likely provided optimal conditions for parasite transmission (Alicata, 1932) resulting in less variation in worm burdens between seasons.

Management Implications

Effects of wildfire and prescribed burning on helminth parasitism have not been well documented. Habitat modifications induced by wildfire can produce optimal conditions for establishment of arthropod intermediate hosts of pathogenic intestinal worms of blue grouse (Bendell, 1974). Prescribed fire for habitat management of Stone's sheep (*Ovis dalli stonei*) decreased *Protostrongylus* sp. larval counts in feces of sheep that utilized burned ranges during winter (Seip and Bunnell, 1985). Cottontail rabbits in our study area experienced similar host-parasite influences from 1987 to 1988. Prescribed burning at CTER occurred in April when infective larvae and eggs should have been abundant in the environment and conditions for transmission were ideal. Burning may have decreased the number of these infective stages available to foraging cottontail rabbits which resulted in lower mean abundances among animals collected from burned sites. This was found to be true of rabbits collected from triclopyr-treated pastures that were burned annually. Spotty, nonuniform burns resulting from a lack of adequate fuel, were probably responsible for higher survival of infective *O. cuniculi* larvae on annually burned tebuthiuron-treated pastures.

This study provided additional evidence that habitat alterations, whether natural or man-induced, can influence host-parasite population relationships in a local area. Host-parasite responses to a given habitat alteration are not always consistent, however my study demonstrates they differ from those responses in untreated habitats. Because habitat modification practices, such as those using herbicides and fire, vary greatly in their effects on vegetation structure and how they are applied, general statements about host-parasite responses may be difficult to make. Longer term research is needed on entire helminth communities to better understand and predict these responses.

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Table 1. Prevalence (number infected/number examined) of *Obeliscoides cuniculi* in cottontail rabbits collected from 5 experimental brush control treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma.

	1987		1988	
Brush treatment	Winter	Summer	Winter	Summer
Tebuthiuron	10/10	10/10	13/13	10/10
Tebuthiuron with annual burning	10/11	10/10	9/10	10/10
Triclopyr	10/10	10/10	10/10	10/10
Triclopyr with annual burning	9/10	10/10	10/10	10/10
Control	9/10	11/11	9/10	10/10
Total	48/51	51/51	51/53	50/50

Table 2. Determination of overdispersion ($\bar{X}/S^2$)[a] and degree of aggregation (K) of Obeliscoides cuniculi individuals in adult cottontail rabbits collected from 5 experimental brush control treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma (n = 180).

	1987[b]				1988[b]				
	Winter		Summer		Winter		Summer		Total
Brush treatment	$\bar{X}/S^2$	K	$\bar{X}/S^2$	K	$\bar{X}/S^2$	K	$\bar{X}/S^2$	K	K
Tebuthiuron	0.091	0.03	0.023	1.30	0.027	0.93	0.044	2.37	0.95
Tebuthiuron with annual burning	0.011	0.54	0.047	2.74	0.153	1.34	0.055	0.45	0.40
Triclopyr	0.005	0.30	0.024	1.25	0.100	1.16	0.030	1.84	0.49
Triclopyr with annual burning	0.146	1.51	0.017	0.74	0.045	0.52	0.061	2.13	0.58
Control	0.027	1.00	0.018	1.12	0.205	1.03	0.019	1.17	0.67

[a] (mean abundance/variance) Where a small number of host individuals harbor many parasite individuals and many of the hosts harbor little to no individuals of a particular parasitic species (based on the frequency distribution of individual parasites).

[b] All variances were significantly larger than respective mean abundances ($P \leq 0.05$)

Table 3. Mean seasonal abundance ($\bar{X} \pm SE$) of *Obeliscoides cuniculi* in cottontail rabbits collected from 5 experimental brush control treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma. Sample size is in parentheses.

	1987				1988			
	Winter		Summer		Winter		Summer	
Brush treatment	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
Tebuthiuron	10.3 ±3.4 (10)	NC[a]	54.4 ±16.1 (10)	3.0 (1)	33.5 ±9.7 (13)	NC	51.9 ±12.2 (10)	32.0 ±31.0 (2)
Tebuthiuron with burn	49.2 ±20.3 (11)	NC	55.4 ±11.4 (10)	101.0 (1)	7.4 ±2.2 (10)	NC	90.6 ±45.2 (10)	67.0 (1)
Triclopyr	56.9 ±34.9 (10)	36.0 (1)	65.4 ±18.3 (10)	54.4 ±49.5 (2)	10.4 ±3.2 (10)	NC	59.3 ±18.1 (10)	75.5 ±23.0 (4)
Triclopyr with burn	8.8 ±2.5 (10)	NC	43.8 ±23.0 (10)	73.0 ±10.0 (5)	11.0 ±4.9 (10)	NC	33.0 ±8.8 (10)	82.3 ±7.4 (3)
Control	36.3 ±11.6 (10)	NC	61.6 ±22.1 (11)	28.5 ±6.1 (4)	4.0 ±1.4 (10)	NC	60.7 ±18.8 (10)	78.0 (1)

[a] NC = no rabbits collected

CHAPTER II

INFLUENCE OF HABITAT MODIFICATION ON INTESTINAL HELMINTH COMMUNITY ECOLOGY OF COTTONTAIL RABBITS (*SYLVILAGUS FLORIDANUS*) IN THE CROSS TIMBERS OF OKLAHOMA

ABSTRACT: The influence of 5 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. Six helminth species were recovered (Dermatoxys veligera, Trichostrongylus calcaratus, Passalurus nonanulatus, Wellcomia longejector, Taenia pisiformis [cystercercus], and Mosgovoyia pectinata americana) from a total of 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 harbored in the intestinal tract of cottontail rabbits were unaffected by brush treatments. M. pectinata americana abundance demonstrated a highly significant increase from winter to summer, conversely, abundance of oxyurid pinworms combined 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 harbored by the eastern cottontail rabbit (Sylvilagus floridanus) show a considerable amount of 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 also across time 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 wildfires and internal and external parasitism of blue grouse (Dendragapus obscurus).

Cottontail rabbits are ubiquitous herbivore components of the cross timbers ecosystem in central Oklahoma. 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). My objective 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

This study was conducted on the Cross Timbers Experimental Range (CTER), which is located approximately 11 km west of Stillwater, Oklahoma. 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 x 0.83 km) fenced experimental pastures, representing 4 replications of 4 brush management treatments, using combinations of herbicide and annual prescribed burning applications and an untreated-control. This provides a 2 x 2 factorial design of 4 replications of 5 treatments (Appendix D). 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), applied aerially at 2.2 kg per ha in March 1983; (2) tebuthiuron applied (as with 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), applied aerially at 2.2 kg per ha in June 1983; (4) triclopyr applied (as with treatment #3) with annual prescribed burning begining in April, 1985; and (5) untreated control. 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 meters above the soil surface) was collected from each pasture within seven caged quadrats (50 x 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 $70^{o}C$ then weighed. Differences between treatments were determined by 2-way analysis of variance.

An attempt was made to collect 5 cottontail rabbits from each of 2 replications for each treatment in winter (January) and summer (July) of 1987. Carcasses were necropsied within 24 hours of collection or frozen until necropsy could be performed. 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 micron sieve and a 25% aliquot was examined. The combined cecal and large intestinal contents were sieved as above and a 10% aliquot was examined. Recovered 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 recovered from our study were deposited in the U. S. National Parasite Collection, Beltsville, Maryland 20705, U. S. A. (Accession Nos. 80495 - 80500).

Data analysis

Abundance, intensity, and prevalence are defined by Margolis et al. (1982). 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 (Bliss and Fisher 1953) has been used to describe the frequency distributions of common ($\geq$25% prevalence) species of intestinal helminths where a small number of host individuals harbor many helminth individuals and many of the hosts harbor little to no individuals of a particular helminth species (Waid et al., 1985; Corn et al., 1985). Overdispersion was indicated when the variance for a particular species was significantly ($\underline{P} \leq$ 0.050) larger than the mean abundance using a chi-square distribution ($\underline{X}^2$, $[S^2/X]$ x 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 analysis of variance using Anscombe's transform (common k estimate), $\log_{10}(x + 1/2k)$, 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) 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 pinworm (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 vs. unburned, tebuthiuron vs. triclopyr, control vs. 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 $P \leq 0.100$ for data analyses. Copies of the raw and rank transformed data are available upon request from Robert L. Lochmiller.

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 ($P < 0.001$) among the control and brush treatments. 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;

Rudolphi, 1819; P. nonanulatus; Skinker, 1931; T. calaratus; Ransom, 1911; and W. longejector; Hannum, 1943) and two species of cestodes (T. pisiformis; Bloch, 1780 and M. pectinata americana; Douthitt, 1915) 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. W. longejector occurred in only 2 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 D. veligera were significantly ($P < 0.050$) higher in adults than juveniles. There were no age-related differences in mean abundances for M. pectinata americana, T. calcaratus, and P. nonanulatus.

Helminth prevalence

Prevalence (Table 1) 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 ($P > 0.100$) in prevalence of T. calcaratus, P. nonanulatus, T. pisiformis, M. pectinata, and W. longejector. There was also no difference ($P > 0.100$) in prevalence between seasons for oxyurid pinworms combined. Prevalence of M. pectinata americana and T. pisiformis infections were significantly affected by experimental brush treatments. Prevalence of M. pectinata americana was higher ($P < 0.010$) on untreated controls (100%) than herbicide- treated pastures (53%). There were no differences (P > 0.100) 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 <0.050) on burned (93%) than on unburned (65%) treatments. No differences (P > 0.100) existed in prevalence of T. pisiformis between untreated controls and herbicide treatments or tebuthiuron and triclopyr treatments. Overall prevalences of D. veligera (19%), W. longejector (2%) , P. nonanulatus (32%), and T. calcaratus (97%) were not affected by brush treatment. Prevalence of oxyurid pinworm infections combined was 47%.

Helminth abundance and intensity

Mean rank abundance and intensity data for helminths recovered from our study showed no significant difference (P > 0.100) between male and female cottontail rabbits (Table 2). However, mean rank abundances of T. calcaratus, M. pectinata americana, and oxyurid pinworms combined showed significant season by sex interactions. T. calcaratus (P < 0.060) and M. pectinata (P < 0.100) infections during summer were higher among females than males, while the reverse was true in winter. Conversely, oxyurid pinworms combined were higher (P < 0.097) among females in winter and higher among males in summer.

Except for T. pisiformis, abundances for all helminths recovered from our study differed significantly between seasons (Table 3). Mean rank abundances were lower for T. calcaratus ($P < 0.001$), and higher for M. pectinata americana ($P < 0.001$) and oxyurid pinworms 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 ($P > 0.100$) between seasons. Mean rank abundances and intensities for all helminths recovered showed no significant relationship ($P > 0.100$) 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 ($P > 0.100$) were appparent between host sexes or among brush treatments

Helminth distribution

All helminth species recovered with the exception of M. pectinata, had variances significantly ($P < 0.050$) larger than respective mean abundances across all treatments and seasons (Table 4), indicating an overdispersed distribution (Bliss and Fisher, 1953). However, variances of M. pectinata americana were not significantly ($P > 0.050$) larger than respective mean abundances in winter, but showed significant ($P < 0.050$) overdispersion in summer. A low range of M. pectinata infection (0 - 4), with only 1 rabbit harboring a burden of 4 worms, was responsible for low variances within winter samples. Analysis of variance for common k estimates revealed significant seasonal effects for the distribution of T. calcaratus ($P < 0.001$), M. pectinata americana ($P < 0.004$), and all oxyurid pinworms combined ($P < 0.017$); however, no significant differences in helminth distribution (k values) were detected among brush treatments. T. pisiformis distribution was not affected ($P > 0.100$) 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 affected the greater change in vegetation by reducing oak (Quercus sp.) and other hardwoods in the overstory and increasing herbaceous understory production. Plant communities of both burned and unburned herbicide-treated pastures has undergone retrogression since 1984 when herbicides were first applied

(Stritzke et al., 1987).

Helminth fauna new to Oklahoma

M. pectinata americana, W. longejector, and D. veligera are reported for the first time in eastern cottontail rabbits from Oklahoma. M. 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). W. longejector was first described by Hannum (1943) from lagomorphs and rodents in Arizona. D. veligera, a common oxyurid pinworm of cottontail rabbits, has been found in Kansas (Franklin et al., 1966) and other locations in the U. S. (Cheatum, 1943; LeDune, 1933; Llewellyn and Handley, 1945; Jacobson et al., 1978; Moore and Moore, 1947; Novelsky and Dyer, 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 parastism

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). T. 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 4.5% reported in cottontail rabbits from Minnesota (Erickson, 1947) and 6.5% from North Dakota (Novelsky and Dyer, 1970). Unlike Cittotaenia sp. infections in cottontail rabbits from Virginia (Jacobson et al., 1978) and Kentucky (Strohlein and Christensen, 1983), no seasonal differences in prevalence of M. pectinata were 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 conopy 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.

T. 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. *T. 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 sp. abundances in cottontail rabbits from Virginia which were similar to this study regarding M. pectinata . 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 my study were also consistent with previous surveys of cottontail rabbits in Virginia (Jacobson et al., 1978).

Nematode parasitsm

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 cottontail rabbits in the southeastern U. S. (Andrews et al., 1980; Jacobson et al., 1978).

Oxyurid pinworms, as with 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 pinworm 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.

Helminth community

Except for T. pisiformis, helminth distribution in cottontail rabbits inhabiting the CTER was influenced most by season. Intrinsic variables such as host behavior and physiological condition, and extrinsic variables such as temperature and humidity may have contributed to seasonal differences in overdispersion of parasites in cottontail rabbits. However, our study indicates that extrinsic variables such as brush treatment can be as important as intrinsic variables in influencing population dynamics of certain helminth species of the cottontail rabbit. Natural successional or management-induced modifications of the habitat can potentially alter host-parasite community relationships in a cross timbers ecosystem. 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.

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Figure 1. Forest floor material collected from 5 brush management treatments on the Cross Timbers Experimental Range.

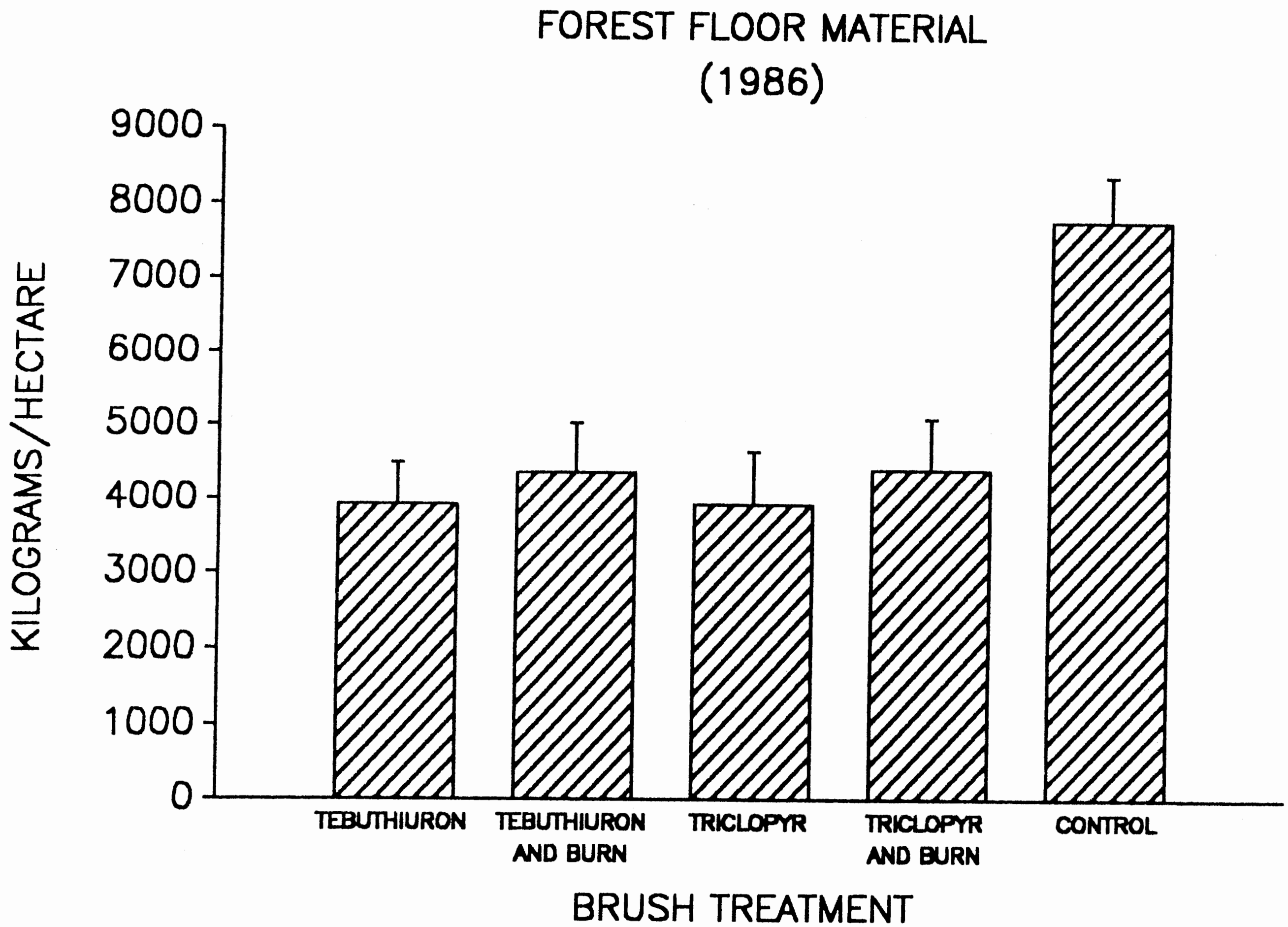
FOREST FLOOR MATERIAL
(1986)
KILOGRAMS/HECTARE
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
TEBUTHIURON
TEBUTHIURON AND BURN
TRICLOPYR
TRICLOPYR AND BURN
CONTROL
BRUSH TREATMENT

Table 1. Prevalence of infection (number infected/number examined) by intestinal helminth parasites recovered from adult cottontail rabbits (n = 88) collected from 5 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
Pinworms (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<0.010) brush treatment effects for winter specimens

[b] Significant (P<0.050) brush treatment effects for summer specimens

Table 2. 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
Pinworms (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 3. Mean abundance and intensity data (standard error) for intestinal helminths recovered from 88 adult cottontail rabbits collected in winter and summer, 1987, from 5 experimental brush treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma.

Brush treatment		*Trichostrongylus calcaratus*		*Mosgovoyia pectinata*		*Taenia pisiformis*		*Passalurus nonanulatus*		Pinworms (total)	
		Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Tebuthiuron	A	90.2 (23.1)	300.0 (66.7)	3.0 (1.3)	0.6 (19.5)	35.0 (19.5)	5.4 (1.5)	78.9 (58.2)	37.0 (37.0)	82.2 (57.6)	37.0 (37.0)
	I	90.2 (23.1)	300.0 (66.7)	3.4 (1.4)	1.2 (0.2)	52.5 (27.1)	6.0 (1.5)	177.5 (120.2)	370.0 (0.0)	123.3 ((83.4)	370.0 (0.0)
Tebuthiuron and burn	A	188.9 (129.8)	403.3 (70.3)	4.6 (2.5)	1.0 (0.4)	10.1 (2.1)	5.1 (1.3)	1060.00 (961.4)	149.1 (119.5)	1092.2 (970.0)	150.9 (118.9)
	I	188.9 (129.8)	403.3 (70.3)	5.9 (3.0)	1.6 (0.4)	11.4 (1.9)	5.6 (1.4)	3180.0 (2778.7)	820.0 (480.0)	1404.3 (124.0)	415.0 (305.0)
Triclopyr	A	96.5 (34.8)	354.2 (107.2)	5.9 (2.4)	0.8 (0.2)	6.5 (2.7)	4.3 (2.4)	418.8 (404.6)	290.0 (211.5)	472.5 (405.6)	290.0 (211.5)
	I	110.3 (36.8)	354.2 (107.2)	5.9 (2.4)	1.0 (0.0)	10.4 (3.1)	6.5 (3.3)	1116.7 (1066.8)	1305.0 (535.0)	630.0 (536.0)	1305.0 (535.0)
Triclopyr and burn	A	272.0 (201.9)	355.2 (113.1)	4.4 (2.3)	0.3 (0.2)	7.4 (2.1)	6.5 (2.7)	2.0 (2.0)	341.0 (313.5)	2.0 (2.0)	31.4 (20.9)
	I	340.0 (245.5)	394.7 (118.5)	5.5 (2.6)	1.0 (0.0)	7.4 (2.1)	8.1 (3.2)	10.0 (0.0)	682.0 (619.8)	10.0 (0.0)	55.0 (33.0)
Control	A	89.1 (22.9)	361.6 (142.1)	2.7 (1.0)	1.4 (0.2)	3.6 (2.1)	8.2 (1.9)	25.7 (20.9)	298.0 (274.0)	341.0 (313.5)	300.0 (273.7)
	I	89.1 (22.9)	361.6 (142.1)	3.8 (1.0)	1.4 (0.2)	6.3 (3.0)	9.1 (1.9)	60.0 (45.1)	745.0 (672.3)	682.0 (619.8)	600.0 (540.6)

A = Abundance

I = Intensity

Table 4. Determination of overdispersion and measure of degree of aggregation of helminth parasites in cottontail rabbits collected from 5 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. k values 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*	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*	----	----	----	----	----	----	----
Pinworms	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

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

CHAPTER III

HELMINTH COMMUNITY ECOLOGY IN COTTON RATS (SIGMODON HISPIDUS) AS INFLUENCED BY HABITAT MODIFICATION IN THE CROSS TIMBERS OF OKLAHOMA

ABSTRACT: Dynamics of gastrointestinal helminth communities of cotton rat (Sigmodon hispidus) populations were monitored in response to 5 experimental brush management treatments using prescribed burning and herbicide applications on the Cross Timbers Experimental Range in Payne County, Oklahoma. 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 5 helminth species: Longistriata adunca, Syphacia sigmodontis, Strongyloides sp., Protospirura muris, and Raillietina sp. Prevalence and abundance of Raillietina sp. and abundance of S. sigmodontis were significantly lower on annually burned pastures compared to unburned pastures. Abundance of L. adunca also showed a significant treatment by season interaction. Abundances of L. adunca in cotton rats decreased from winter to summer on annually burned pastures while increasing on other pastures. Cotton rats from control pastures had higher prevalences of Raillietina sp. in winter and S. sigmodontis in both summer and winter than did brush-treated pastures. Distribution of all helminths was overdispersed. 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. These results indicate that man-induced habitat modifications can alter host-parasite relationships in the community.

Key words: Cotton rat, Sigmodon hispidus, Habitat modification, parasitism, helminths, 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 blacktailed 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.

Cotton rats (Sigmodon hispidus) are important small mammal components of the cross timbers ecosystem in central Oklahoma. Herbicide applications and 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). I 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, I examined the influences of herbicide and 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 in Payne County. 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 x 0.83 km) fenced experimental pastures, representing 4 replications of 4 brush management treatments, using combinations of herbicide and annual prescribed burning applications, and an untreated control

(Appendix D). This provides a 2 x 2 factorial experimental design of 4 replications of 5 treatments. The 5 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), 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), applied aerially at 2.2 kg per ha in June 1983; (4) triclopyr applied (as with #3) with annual prescribed burning in April, beginning in 1985; (5) untreated control. 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.

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, I also collected animals from untreated cross timbers rangeland on nearby (within 2.5 km) research lands to serve as controls. Cotton rats were sampled by removal snap-trapping using a randomly placed 8 X 8 transect grid with 15 meter spacing between trap stations within each pasture. Snap traps were baited with a peanut butter-rolled oats mixture and apples for 3 consecutive days. Cotton rats were frozen immediately after collection and later necropsied and eviscerated as time allowed. Eviscerated intestinal contents were sieved with a 150 micron filter and diluted 10 or 50%, depending upon volume of contents, for enumeration of nematodes. Total recovery of tapeworms and stomach worms was attempted.

Nematodes were stored in 70% ethanol and examined in lactophenol wetmounts. Cestodes were fixed in acetic acid-formalin ethyl alcohol, stained in Carmine and mounted in permount. Representative samples of helminths recovered from this study have been deposited in the U. S. National Parasite Collection, Beltsville, Maryland 20705, U.S.A. (Accession nos. 80566-80570).

<u>Data analysis</u>

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

Overdispersion is 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, $Log_{10}(x + 1/2k)$, 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) 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). Apriori specific contrasts were used to compare variation among brush treatment components (burned vs. unburned, tebuthiuron vs. triclopyr and control vs. treatment). 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 is 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* Chandler, 1932; *Strongyloides* sp. Grassi, 1879; *P. muris* Gmelin, 1790; *Syphacia sigmodontis* Quentin and Kinsella, 1972) and one cestode (*Raillietina* sp. Fuhrmann, 1920) were recovered from 113 (68 male and 45 female) cotton rats (Table 1). All four helminth species were recovered from cotton rats collected from control and annually burned tebuthiuron pastures, and these were the only treatments from which *P. muris* was recovered. *Syphacia sigmodontis* was not recovered from cotton rats in annually burned triclopyr treatments. *Raillietina* sp., *L. adunca*, and *Strongyloides* sp. were recovered from cotton rat populations on all brush treatments.

Prevalence

Prevalence of S. sigmodontis and Raillietina sp. infections in cotton rat populations were significantly ($P < 0.050$) influenced by experimental brush treatments (Table 2). Prevalence of S. sigmodontis infection was greater ($P < 0.050$) in populations from control (38.5%) than treated (14.0%) pastures. Prevalence of Raillietina sp. infections was greater ($P < 0.050$) on control (53.8%) than brush treated (26.0%) pastures and greater ($P < 0.005$) on tebuthiuron (34.0%) than triclopyr-treated (18.9%) pastures. Cotton rat populations from unburned experimental treatments (40.0%) also had a greater ($P < 0.005$) prevalence of Raillietina sp. infection than those collected from burned (14.6%) pastures.

Prevalence of P. muris was high in cotton rats collected from control pastures in winter (62.5%); only one cotton rat from brush-treated habitat (annually burned tebuthiuron) was infected with P. muris. Brush treatments had no significant influence ($P > 0.100$) on the prevalence of Strongyloides sp. in cotton rat populations. However, prevalence was affected by season, being greater ($P < 0.050$) in winter (29.3%) than summer (21.8%). Prevalences of other helminths were not significantly ($P > 0.100$) affected by season.

Helminth abundance and intensity

Mean rank abundances of Raillietina sp. were significantly ($\underline{P}$ < 0.001) affected by brush treatment. Cotton rats collected from unburned pastures had lower ($\underline{P}$ < 0.001) abundances of Raillietina sp. compared to burned pastures (Table 3). Mean rank abundances of Raillietina sp. were also greater ($\underline{P}$ < 0.043) in cotton rats from tebuthiuron-treated than triclopyr-treated pastures. Abundances of Raillietina sp. were not different ($\underline{P}$ > 0.100) between control and brush-treated pastures. Abundance of Raillietina sp. was also influenced by host sex, being greater ($\underline{P}$ < 0.039) in male than female cotton rats. Season had no influence ($\underline{P}$ > 0.100) on the abundance of Raillietina sp. in cotton rats.

Mean rank abundance of S. sigmodontis differed significantly ($\underline{P}$ < 0.005) among brush treatments as well. Abundances of S. sigmodontis were greater ($\underline{P}$ < 0.016) for cotton rats collected from unburned than burned pastures. Abundances of S. sigmodontis were also greater ($\underline{P}$ < 0.012) for cotton rats obtained from control pastures compared to brush treated pastures. A treatment by season interaction ($\underline{P}$ < 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 was no significant ($\underline{P}$ > 0.100) difference in abundances between seasons or host sexes for this parasite. Triclopyr-treated pastures had significantly greater ($\underline{P}$ < 0.016) abundances than tebuthiuron-treated pastures. A significant ($\underline{P}$ < 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 pastures while inreasing for those from unburned pastures. 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 affected by brush treatment ($P > 0.456$), season ($P > 0.773$), or host sex ($P > 0.774$). Mean abundance of P. muris infection was 2.6 $\pm$ 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 (clumping) throughout the year across all treatments. Analysis of distribution (k) data was only performed on Strongyloides sp. and L. adunca; distributions of other helminths were not suitable for statistical analysis (table 4). Overdispersion of Strongyloides sp. was not significantly affected by host sex ($P > 0.815$), season ($P > 0.965$), or brush treatment ($P > 0.686$). However, distribution of Strongyloides sp. did show a significant ($P < 0.004$) treatment by season interaction. Overdispersion of Strongyloides sp. in cotton rat populations from triclopyr-treated pastures was greater in winter than summer, while the reverse was true for cotton rats from tebuthiuron-treated pastures. 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 where overdispersion in summer was greater for cotton rats from herbicide-treated pastures than controls. No significant differences were found in the distribution of *L. adunca* due to host sex ($P > 0.176$) or season ($P > 0.397$).

Helminth community

Multivariate analysis of variance 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 influenced by season ($P < 0.220$) or host sex ($P < 0.230$). Specific contrasts between brush treatment categories indicated that helminth communities harbored by cotton rat populations differed in mean rank abundance between contol and treated ($P < 0.020$), burned and unburned ($P < 0.003$), and tebuthiuron and triclopyr ($P < 0.025$) pastures.

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. Prescribed burning removes litter and increases forage quality while favoring tolerant vegetation (Grelen and Epps, 1967). Fleharty and Mares (1973) found that S. hispidus of central Kansas prefered vegetative communities composed of forbs 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.

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 recovered 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 the 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). P. muris (syn. Mastophorus muris) is a spirurid stomach worm of rodents and has been identified from cotton rats in Florida (Kinsella, 1974), Texas (Mollhagen, 1978), and Virginia (Seidenberg et al., 1974). *Longistriata adunca*, a trichostrongylid nematode in the small intestine, was the most widely distributed and prevalent helminth of our study, and has been reported from Texas (Melvin and Chandler, 1950; Scott and Blynn, 1952), North Carolina (Coggins and McDaniel, 1975), and Virginia (Seidenberg et al., 1974).

Helminths with two hosts

Raillietina sp. was the only cestode recovered from cotton rats on the CTER and could be either *R. bakeri* or *R. sigmodontis*. Prevalence of *Raillietina* sp. recorded from a previous study in Texas (Mollhagen, 1974), was similar to ours. Prevalences higher than those observed on the CTER have been reported in surveys in Florida (Kinsella, 1978) and North Carolina (Coggins and McDaniel, 1975). Abundance of *Raillietina* sp. recovered from our study was considerably less than that reported from Virginia (Seidenberg et al., 1974) and 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 previously reported 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 was probably a reflection of the availabilty of intermediate hosts. Insects from the orders diptera (house flies), coleoptera (meal worms and cockroaches), and hymenoptera (ants) vector Raillietina sp. infections (Horsfall, 1938; Ackert, 1922), while spirurids (P. muris) are typically vectored by orthopterans and coleopterans (Yamagouti, 1961). 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 (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 vectors of P. muris and Raillietina sp. probably contributed to the low prevalence of these helminths in cotton rat populations from brush treated pastures. Host sex effects on Raillietina sp. are documented (Coggins and McDaniel, 1975) and consistent with my findings.

Helminths with one host

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 McDaniels, 1974) were much lower than mine. Abundance data suggested that triclopyr-treated pastures provided more optimal 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 (ie 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 life cycle. _Strongyloides_ _sigmodontis_ filariform larvae 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 my 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 were similar to those of Raillietina sp. Both the direct affect of fire on deposited eggs and subsequent modifications of the microclimate as a result of litter and vegetation structure changes in the habitat were probably the primary factors influencing infection in cotton rats (Bendell, 1974; Issac, 1963; Seip and Bunnell, 1985).

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.

Observed variation in helminth community dynamics in cotton rats across brush treatments on the CTER is consistent with previous studies comparing helminth communities across differing habitat types. Kinsella (1974) found that trematodes of cotton rats, vectored by molluscs, 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 my 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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Table 1. Helminth species richness for 113 adult cotton rats (*Sigmodon hispidus*) collected from 5 experimental brush treatments during summer and winter, 1986 on the Cross Timbers Experimental Range, Payne County, Oklahoma.

	Brush Treatment				
Parasites	Tebuthiuron	Tebuthiuron with burn	Triclopyr	Triclopyr with burn	Control
Longistriata adunca	+	+	+	+	+
Strongyloides sp.	+	+	+	+	+
Syphacia sigmodontis	+	+	+	−	+
Protospirura muris	−	+	−	−	−
Raillietina sp.	+	+	+	+	+

(+) = Present

(−) = Absent

Table 2. Prevalence of infection (number infected/number examined) by intestinal helminth parasites recovered from 113 adult cotton rats (Sigmodon hispidius) collected from 5 experimental brush treatments at the Cross Timbers Experimental Range, Payne County, Oklahoma, during summer and winter, 1986.

	Brush Treatment										
	Tebuthiuron		Tebuthiuron with burn		Triclopyr		Triclopyr with burn		Control		
Parasites	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Total
Longistriata adunca	10/12	10/10	11/12	11/13	14/15	14/15	11/11	12/12	4/5	8/8	92%
Strongyloides sp.	4/12	3/10	1/12	6/13	5/15	4/15	2/11	3/12	0/5	1/8	26%
Syphacia sigmodontis	4/12	0/10	3/12	0/13	4/15	3/15	0/11	0/12	0/5	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%

Table 3. Mean abundance and intensity data (standard error) for intestinal helminths recovered from 113 adult cotton rats (*Sigmodon hispidus*) collected from 5 experimental brush treatments at the Cross Timbers Experimental Range, Payne County, Oklahoma, during summer and winter, 1986.

Brush Treatment		*Longistriata adunca*		*Strongyloides* sp.		*Syphacia sigmodontis*		*Raillietina* sp.	
		Summer	Winter	Summer	Winter	Summer	winter	Summer	Winter
Tebuthiuron	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	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)	1348.7 (1327.7)	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)	2037.5 (1465.5)	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 = Abundance

I = Intensity

Table 4. Determination of overdispersion and measure of aggregation (k) for the distribution frequencies of helminth species recovered from 113 adult cotton rats (<u>Sigmodon</u> <u>hispidus</u>) collected from 5 experimental brush treatments at the Cross Timbers Exprimental Range during summer and winter, 1986. k values 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	Overall
<u>Longistriata</u> <u>adunca</u>	0.54*	1.24*	0.66*	0.81*	0.52*	1.48*	0.70*	3.19*	3.82*	0.60*	0.61*
<u>Strongyloides</u> sp.	0.20*	0.20*	0.11*	0.39*	0.38*	0.20*	0.32*	0.19*	NE	0.25*	0.18*
<u>Syphacia</u> <u>sigmodontis</u>	0.23*	NE	0.08*	NE	0.11*	0.15*	NE	NE	0.20*	0.20*	0.03*
<u>Raillietina</u> sp.	0.50*	0.74*	NE	NE	NE	NE	0.35*	NE	NE	NE	0.19*

* = Variance is significantly (X^2, $P < 0.050$) larger than the mean abundance

NE = Not estimatable

CHAPTER IV

GASTROINTESTINAL HELMINTH COMMUNITY OF EASTERN WOODRATS (*NEOTOMA FLORIDANA*) IN RESPONSE TO HABITAT MODIFICATION IN CENTRAL OKLAHOMA

ABSTRACT: Dynamics of the gastrointestinal helminth communities of eastern woodrat (Neotoma floridana) populations were monitored in response to 5 experimental brush management treatments applied to typical cross timbers rangeland in central Oklahoma. A total of 99 eastern woodrats (55 female, 44 male) was collected from experimental pastures in winter and summer from 1986 to 1987. Three helminth species were recovered: Bohmiella wilsoni, Longistriata neotoma, and Trichuris muris. Prevalence of infection with L. neotoma in eastern woodrat populations was higher in summer than winter. Conversely, prevalences of B. wilsoni and T. muris were higher in winter than summer. Experimental brush treatments significantly influenced winter prevalences of L. neotoma and T. muris in eastern woodrat populations. Prevalence of L. neotoma was higher on tebuthiuron treatments compared to triclopyr-treated pastures and prevalence of T. muris was higher on burned than unburned pastures. Abundances for B. wilsoni and L. neotoma differed between seasons. Abundance of L. neotoma infection was significantly affected by brush treatment, where woodrats from untreated controls had higher numbers than those from brush treated pastures. Distributions of L. neotoma infections in eastern woodrat populations were most influenced by season and brush treatment, and distributions of B. wilsoni infections were only influenced by season.

Key words: Brush control, Neotoma floridana, eastern

woodrats, Longistriata neotoma, Bohmiella wilsoni, Trichuris muris, helminth population dynamics.

INTRODUCTION

Considerable variation in helminth community composition exists within host populations compared across geographic regions in North America (Davidson, 1976; Pence et al., 1983; Andrews et al., 1980). This geographic variation is believed to be attributed to differences in extrinsic habitat variables such as soil moisture (Kinsella, 1974), resident plant communities (Martin and Huffman, 1980), and man-made perterbations (Jirous, 1985). However, extrinsic habitat factors vary not only across the geographic range of a host species but also across time within the habitat of a resident population. Natural successional and man-induced changes of the habitat can potentially alter a variety of extrinsic habitat factors, both abiotic and biotic components. For example, Issac (1963) and Bendell (1974) reported changes in helminth communities of blacktailed deer (Odocoileus hemionus columbianus) and blue grouse (Dendragapus 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.

In addition to using fire, a variety of herbicides and mechanical methodologies are commonly applied techniques for modifying the composition and structure of rangeland habitats (Scifres, 1980). These range management techniques can influence vertebrate and invertebrate populations which can serve as primary and intermediate hosts for a variety of parasites. Herbicide and fire applications have been shown to greatly influence the diversity and abundance of small mammals (Kirkland, 1978; Santillo, 1989) and arthropods (Warren et al., 1987; Seastedt, 1984a and 1984b; Guerra et al., 1982).

Similar range management techniques are presently used on brush-dominated rangelands in the cross timbers of Oklahoma to improve livestock grazing potential (Engle, 1987). The cross timbers vegetation type is dominated by post oak (Quercus marilandica) - blackjack oak (Q. stellata) woodlands and supports a wide variety of small mammals. The impact of these range modifications on host-parasite community relationships are currently unknown. The objective of my study was to examine the influence of these brush management strategies on the gastrointestinal helminth community of eastern woodrat (Neotoma floridana) populations in central Oklahoma. I analyzed the distribution, abundance, intensity, and prevalence of infections in woodrat populations inhabiting rangelands treated with combinations of herbicide and fire.

MATERIALS AND METHODS

Study area

Eastern woodrats were collected on the Cross Timbers Experimental Range (CTER), located approximately 11 km west of Stillwater, Oklahoma. The CTER is a 648-ha research area composed of blackjack oak - post oak 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 x 0.83 km) fenced experimental pastures, representing 4 replications of 4 brush management treatments, using combinations of herbicide and annual prescribed burning applications, and an untreated control (Appendix D). This provides a 2 x 2 factorial experimental design of 4 replications of 5 treatments. The 5 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) 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) applied aerially at 2.2 kg per ha in June 1983; (4) triclopyr applied (as with #3) with annual prescribed burning in April, beginning in 1985; (5) untreated control. All experimental pastures were moderately grazed by cattle during the 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 by understory woody species reduced the production of herbaceous plants after the triclopyr treatment.

Data collection

Populations of eastern woodrats were sampled over a two year period (1986 and 1987) with collections in summer (July - September) and winter (December - January). Popuations were sampled within upland post oak-blackjack oak savannas by removal snap-trapping using a randomly placed 8x8 transect grid with 15m spacing between grid points. Two replications of each of 5 experimental treatments were sampled per season. To avoid depleting numbers of woodrats in a local area, trapping grids were always relocated to areas previously unsampled before beginning another sampling period. Snap traps were baited with peanut butter and woodrats were removed daily from traps for 3 consecutive days. Woodrats were returned to the laboratory and stored frozen until necropsies could be performed. Intestinal tracts were eviscerated and contents sieved through a 150 micron filter. Filtered contents were diluted 10 or 50%, depending on the volume, for enumeration of helminths. The stomach was eviscerated and total contents examined for stomach worms. The entire small intestine and liver were examined for tapeworms. A dissecting microscope was used in examining gastrointestinal contents.

Nematodes were stored in 70% ethanol and examined in lactophenol wetmounts. Representative samples of helminths recovered from this study have been deposited in the U. S. National Parasite Collection, Beltsville, Maryland 20705, U.S.A. (Accession nos. 80572-80574).

Data analysis

The terms abundance, intensity and prevalence are defined by Margolis et al. (1982). Only adult eastern wooodrats were used for nematode recovery and all available hosts were examined, resulting in a data set of 99 specimens.

Overdispersion is defined by Bliss and Fisher (1953) and is used to describe the frequency distributions of common (>25% 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 ($\underline{P} \leq 0.050$) 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, $Log_{10}(x + 1/2k)$, of abundance data (Bliss and Owen, 1958). Overdispersed helminth abundances for the 99 sample data set were independently rank transformed (Conover and Iman, 1981; PROC RANK, Statistical Analysis Systems, 1985, SAS Institute, Raleigh, North Carolina) 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 year, and sex were examined with a factorial analysis of variance for the ranked abundances of recovered nematode species (PROC GLM, SAS). Specific contrasts were used to compare variation among brush treatment components (burned vs. unburned, tebuthiuron vs. triclopyr and control vs. treatment). 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 among experimental brush treatments and seasons. T. muris infections were too infrequent, with low intensities for analysis of abundance and distribution data.

Statistical significance is set at P < 0.100). Copies of the raw and rank transformed data are available upon request from Robert L. Lochmiller.

RESULTS

Prevalence

Three nematode species; Longistriata neotoma Murphy, 1952; Bohmiella wilsoni Lucker, 1943; and Trichuris muris Schrank, 1788; were recovered from a total of 99 (44 male, 55 female) eastern woodrats. No cestode or trematode helminths were recovered. These 3 nematodes were represented on all experimental brush treatments.

Prevalence (Table 1) for B. wilsoni (51.5%), L. neotoma (74.7%), and T. muris (21.2%) were not significantly influenced by year of collection, hence, these data were pooled for analysis of season and treatment effects. Prevalence of all 3 species of nematodes recovered were significantly influenced by season of collection. Bohmiella wilsoni and T. muris were found more frequently in woodrat populations sampled in winter ($P < 0.001$), while L. neotoma was most prevalent in summer ($P < 0.025$).

Experimental brush treatments influenced the number of hosts infected with L. neotoma and T. muris on the CTER (Table 1). Prevalence of L. neotoma infection in winter was significantly influenced by experimental brush treatment ($P < 0.025$) where woodrat populations inhabiting pastures treated with tebuthiuron had a higher ($P < 0.100$)

prevalence (76.5%) than those from triclopyr-treated pastures (47.8%). Prevalence of _T. muris_ infection was higher (_P_ < 0.100) in woodrat populations from burned pastures (56.3%) compared to unburned pastures (28.6%) in winter. Prevalence of _B. wilsoni_ infection showed no significant relationship to experimental brush treatment.

Abundance and intensity

Year of collection had no significant (P > 0.100) influence on mean abundances or intensities (Table 2) of _B. wilsoni_ and _L. neotoma_ so we pooled the data across years for analysis of the main effects of treatment, season, and host sex. Mean rank abundances for _B. wilsoni_ were higher (_P_ < 0.001) in winter than summer. Mean rank abundance of _L. neotoma_ infection was higher (_P_ < 0.013) in summer than winter, and a treatment by season interaction (_P_ < 0.012) was indicated by a significant (_P_ < 0.002) brush treatment effect in winter but not in summer (_P_ > 0.150). Mean rank abundances of _L. neotoma_ infections in winter were higher on untreated control pastures (_P_ < 0.018) than herbicide-treated pastures. Host sex had no effect (_P_ > 0.100) on nematode abundance.

Helminth distribution

Frequency distributions (Table 3) for all helminths recovered in our study revealed variances higher ($P \leq 0.050$) than their respective mean abundances, indicating overdispersion (Bliss and Fisher, 1953). The degree of overdispersion for _B. wilsoni_ and _L. neotoma_ was strongly influenced by season (*P* < 0.001). Overdispersion of *B. wilsoni* infections was greater in summer than winter and *L. neotoma* infections were more overdispersed in winter than summer. Overdispersion of *L. neotoma* infections was influenced by a treatment by season interaction (*P* < 0.001). Analysis of variance for *L. neotoma* overdispersion in winter indicated a significant (*P* < 0.001) brush treatment effect. Contrasts showed a greater degree (*P* < 0.021) of *L. neotoma* overdispersion in herbicide-treated pastures than in untreated controls, and greater overdispersion in triclopyr than tebuthiuron-treated pastures (*P* < 0.086). The effects of experimental brush treatment on overdispersion of *L. neotoma* were not significant (*P* > 0.200) for infections in summer and *B. wilsoni* distribution was not affected (*P* > 0.720) by brush treatment. Distribution was not significantly (*P* > 0.100) affected by host sex for any helminth species recovered.

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 (Grelen and Epps, 1967), and tends to promote grass production (Engle, 1987). Burning is also used as a means of suppressing resprouting tendencies of woody species following applications of herbicides (Scifres, 1980). In general, tebuthiuron and triclopyr herbicide applications altered vegetation on the CTER by reducing oak (Quercus sp.) and other hardwoods in the overstory and increasing herbaceous understory production. Plant communities on all brush-treated experimental pastures have undergone some succession since 1983 when herbicides were first applied (Stritzke et al., 1987).

Helminth community

The only documented survey of helminths of eastern woodrats within the cross timbers region was conducted by Murphy (1952), on sites in close proximity to mine (<5 km). Rainey (1956) examined several woodrats in Kansas, finding no internal helminths. Additional literature about helminth parasitism in wild eastern woodrat populations is evidently unavailable.

Longistiata neotoma (trichostrongylidae) was the most frequently encountered and abundant nematode recovered from eastern woodrats on the CTER. Prevalence of L. neotoma recorded from a previous survey in Oklahoma (Murphy, 1952) was much lower than mine. Higher prevalences of L. neotoma in eastern woodrat populations sampled in summer could be associated with the availability of preferred food resources and higher host densities (McMurry, 1989) compared to winter. Eastern woodrats on the CTER preferred diets composed mainly of eastern redcedar during winter and forbs in summer, with grasses comprising only a minor component

(McMurry, 1989). Trichostrongyle larvae are transmitted to the host by ingestion of infective vegetation (Soulsby, 1982). Also, infective larvae in this family require microhabitats provided by soil and herbage for molting (Soulsby, 1982). This would probably make forb vegetation a better medium than eastern redcedar for L. neotoma transmission to eastern woodrats on the CTER. Longistriata neotoma infections in winter could have been acquired from the previous summer or fall when forbs comprised a greater component of the eastern woodrat diet, and maintained by close association of the host with infective material in the den.

Eastern woodrat dens on the CTER were distributed unevenly across the study area and were found most often in habitats with abundant woody brush, rocky outcrops, and fallen trees and branches. This is consistent with woodrat habitat preferences in Oklahoma reported by Murphy (1952). Because of differences in efficacy and selectivity of herbicides (Engle et al., 1987), triclopyr-treated pastures had greater structural complexity as a result of dense shrub cover compared to tebuthiuron-treated pastures, and provided more optimal habitat for den-building (Birney, 1973). Woodrat den distribution on tebuthiuron-treated pastures tended to be more concentrated than those on triclopyr-treated pastures due to the clumping of resources on these typically open, grass-dominated habitats. Higher prevalences of L. neotoma in tebuthiuron-treated pastures could have been associated in part with this concentration of hosts. This could also account for observed differences in degree of overdispersion between these two treatments. However, alteration of microclimatic conditions by experimental brush treatments could also have contributed to these differences. Santillo et al. (1989) found that soil surface temperatures were higher than air temperatures on herbicide (glyphosphate)-treated sites and lower than air temperatures on untreated sites. Ewing and Engle (1988) found similar differences in surface temperatures between burned and unburned sites. Higher surface temperatures on burned and unburned herbicide-treated pastures may have adversely influenced development of _L_. _neotoma_ larvae.

Bohmiella _wilsoni_ (trichostrongylidae) has been reported from gray squirrels (_Sciurus_ _carolinensis_) in southeastern United States (Parker, 1968; Parker and Holliman, 1971; Davidson, 1976) but very little has been documented for woodrats. Murphy (1952) provided the first description of _B_. _wilsoni_ in eastern woodrats and found prevalences similar to mine. The high prevalence of _B_. _wilsoni_ on the CTER suggests that the eastern woodrat is an important primary host for this helminth. Although information on the abundance of this stomach worm in woodrat populations from other localities is not available, I would expect future surveys in other localities to reveal that _B_. _wilsoni_ is a common parasite of this rodent. Apparently, information regarding seasonal trends in prevalence, abundance, and distribution of B. wilsoni is not available.

Trichuris muris (trichuridae) has been reported from the large intestine of eastern woodrats in Oklahoma (Murphy, 1952). Prevalence and abundance of this worm were low in comparison to other species in the helminth community. My results are inconsistent with current research which has suggested that frequent burning decreases parasitism with selected helminths with both direct (Soulsby, 1982) and indirect (Seip and Bunnell, 1985) life cycles. However, Bendell (1974) found that over the long-term (12 years post-burn) burning can increase helminth diversity in blue grouse. It is unclear why prevalence of T. muris, which has a direct life cycle, in eastern woodrat populations on the CTER was positively influenced by prescribed burning. Prescribed burning may have altered habitat use patterns of eastern woodrats so that foraging activities were concentrated, increasing the likelyhood of infection. Similar to B. wilsoni, information about seasonal trends in T. muris parasitism is evidently unavailable.

Andrya sp. and Taenia taeniaformis were reported in woodrats in Oklahoma by Murphy (1952) yet were not found in my study. Andrya sp. is an anoplocephaline tapeworm reported from rabbits (Lepus sp. and Oryctolagus sp.; Arnold, 1938), cotton rats (Sigmodon hispidus; Melvin and Chandler, 1950), and other small mammals (Yamagouti, 1961). Anoplocephaline cestodes utilize arthropods as intermediate hosts which have been found to be adversely affected by brush treatment (Warren et al., 1987; Seastedt, 1984b; Guerra et al., 1982). This, in addition to their presumable low (<5%) prevalence in eastern woodrats (Murphy, 1952), could explain why this cestode was not found in my study. Taenia taeniaformis infects felids as an adult tapeworm, utilizing small mammals as intermediate hosts (Soulsby, 1982) and is extensively reported in the liver of cotton rats (Melvin and Chandler, 1950; Kinsella, 1974; Mollhagen, 1978; Martin and Huffman, 1980). Taenia taeniaformis was also not recovered from cotton rats (Sigmodon hispidus) collected on the CTER during the same period of collection.

Species richness of the gastrointestinal helminth community of eastern woodrats on the CTER was lower than that reported by Murphy (1952). The cestode component of the community was completely absent on the CTER. It is interesting that all helminths we recovered from eastern woodrats demonstrated direct life cycles and helminth communities were dominated by trichostrongyles. Trichostrongyle infections of eastern woodrats in my study were very sensitive to the influences of season and habitat modification by brush treatment. These observations support the assessments of Pence and Winberg (1984) that extrinsic factors such as season and habitat are sometimes as important as intrinsic factors (host physiologic condition, behavior) in determining distribution of certain helminth species.

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Table 1. Prevalence of infection (number infected/number examined) by intestinal helminth parasites recovered from 99 eastern woodrats (*Neotoma floridana*) collected from 5 experimental brush treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma, in winter and summer, 1986 and 1987.

	B. wilsoni		*L. neotoma*		*T. muris*	
	Summer	Winter	Summer	Winter	Summer	Winter
Tebuthiuron	4/9	7/11	8/9	10/11	1/9	3/11
Tebuthiuron and burn	3/9	3/6	8/9	3/6	1/9	3/6
Triclopyr	7/15	9/13	13/15	4/13	0/15	3/13
Triclopyr and burn	3/13	9/10	9/13	7/10	1/13	6/10
Control	3/9	4/4	8/9	4/4	1/9	2/4
Overall	51.5%		74.7%		21.2%	

Table 2. Abundance and Intensity data (standard error) for intestinal helminths recovered from 99 adult eastern woodrats (Neotoma floridana) collected from 5 experimental brush treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma, in summer and winter, 1986 and 1987.

Brush treatment		*B. wilsoni*		*L. neotoma*		*T. muris*	
		Summer	Winter	Summer	Winter	Summer	Winter
Tebuthiuron	A	10.3 (9.0)	5.1 (1.5)	42.2 (11.4)	53.3 (18.0)	0.1 (0.1)	3.3 (2.9)
	I	23.3 (19.7)	8.0 (1.3)	47.5 (11.5)	58.6 (19.0)	1.0 (0)	12.0 (10.0)
Tebuthiuron and burn	A	2.3 (1.5)	2.7 (1.3)	70.7 (24.4)	17.3 (10.7)	0.4 (0.4)	0.7 (0.3)
	I	7.0 (3.5)	5.3 (1.2)	79.5 (25.8)	34.7 (16.4)	4.0 (0)	1.3 (0.3)
Triclopyr	A	2.5 (1.3)	9.4 (2.9)	58.9 (9.5)	8.6 (5.6)	0	0.6 (0.3)
	I	5.4 (2.3)	13.6 (3.3)	68.0 (8.4)	28.0 (15.1)	0	2.7 (0.7)
Triclopyr and burn	A	2.5 (1.6)	11.4 (3.1)	37.4 (13.8)	48.2 (19.8)	0.2 (0.2)	4.0 (1.9)
	I	11.0 (4.0)	12.7 (3.1)	54.0 (17.4)	68.9 (24.6)	2.0 (0)	6.7 (2.8)
Control	A	12.9 (8.0)	23.0 (14.2)	90.7 (24.9)	389.0 (308.2)	0.1 (0.1)	5.8 (5.4)
	I	29.0 (15.2)	30.7 (16.8)	102.0 (25.2)	389.0 (308.2)	1.0 (0)	11.5 (10.5)

A = Abundance

I = Intensity

Table 3. Measure of overdispersion (k) for the distribution frequencies of intestinal helminth species recovered from 99 adult eastern woodrats (*Neotoma floridana*) collected from 5 experimental brush treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma, in summer and winter, 1986. k values derived from Bliss and Fisher (1953).

Brush treatment	*B. wilsoni*		*L. neotoma*		*T. muris*	
	Summer	Winter	Summer	Winter	Summer	Winter
Tebuthiuron	0.15	1.41	1.58	0.81	NE	0.12
Tebuthiuron and burn	0.28	0.94	0.94	0.45	0.14	NE
Triclopyr	0.29	0.88	2.66	0.19	NE	0.40
Triclopyr and burn	0.22	1.57	0.57	0.60	0.14	0.48
Control	0.29	0.68	1.49	0.40	NE	0.29
Overall	0.13	0.62	1.13	0.11	0.09	0.17

NE = not estimatable

CHAPTER V

BOT FLY, *CUTEREBRA* SP. (DIPTERA: CUTEREBRIDAE), INFECTIONS OF SMALL MAMMAL COMMUNITIES AS INFLUENCED BY HERBICIDE AND FIRE APPLICATIONS

ABSTRACT: The impact of habitat alterations created by 5 brush manangement systems (herbicide applications with or without prescribed burning) on Cuterebra sp. infections in a host community ($\underline{n}$ = 811) of small mammals was examined on typical cross timbers rangeland in Payne County, Oklahoma from summer 1986 to 1988. Prevalence of Cuterebra sp. infection in host communities inhabiting tebuthiuron-treated pastures was greater than those on triclopyr-treated pastures in 1986. Prevalence of Cuterebra sp. infection on unburned pastures was also greater than annually burned herbicide-treated pastures in 1986. Cuterebra sp. infections were related to host age in eastern woodrats (Neotoma floridana) and white-footed mice (Peromyscus leucopus), and sex in only eastern woodrats. Host density did not influence prevalence or intensity of Cuterebra sp. infections, and prevalence of infections among small mammal host species were not correlated. Intensity of infection was not influenced by habitat modification, host sex, or age. Prescribed burning might have killed soil dwelling larvae or created unfavorable microclimates for development, therefore reducing prevalence of Cuterebra sp. infection. Tebuthiuron-treated pastures probably provided more suitable topographical summits for Cuterebra sp. aggregation.

Key words: Bot fly, Cuterebra sp., Cuterebridae, Myiasis, habitat modification, triclopyr, tebuthiuron, prescribed burning, small mammals, cottontail rabbits.

INTRODUCTION

Many species of small mammals are commonly infected with larval bot flies of the genus Cuterebra (Diptera: Cuterebridae). A considerable volume of published literature exists on cuterebrid infections and their relationship to host behavior (Catts, 1967; Smith, 1978a), vulnerability to predation (Smith, 1978b), pathology (Payne and Cosgrove, 1966; Capelle, 1971), age and sex (Hunter et al., 1972), and specificity of infection (Catts, 1965). However, knowlege regarding bot fly parasitism associated with differing habitat types and characteristics is limited.

Bennett (1972) compared bot fly parasitism in chipmunks (Tamius striatus) between second-growth mixed forests and mature coniferous forests in Ontario, Canada. He reported greater prevalence and intensity of Cuterebra emasculator infections in chipmunks from second-growth than in mature forests. Hensley (1976) found the prevalence of Cuterebra fontinella infections in woodmice (Peromyscus leucopus) to be greater in forested or brushy habitats than old fields. He did not find any association with intensity of infection and habitat type.

Herbicide application, prescribed burning, and a variety of mechanical methodologies are commonly used techniques for modifying the composition and structure of rangelands throughout Oklahoma and Texas (Scifres, 1980). These range management techniques have been found to influence resident vertebrate and invertebrate populations (Warren et al., 1987; Santillo et al., 1989;). For example, herbicide and fire applications can dramatically influence the abundance and diversity of small mammals (Kirkland, 1978; Santillo et al., 1989) and arthropods (Seastedt, 1984a and 1984b; Guerra et al., 1982). Also, Dipteran populations in the U. S. are known to be influenced by prescribed burning (Warren et al., 1987) and various silvicultural practices (Hall and Thomas, 1979).

Range management techniques including herbicide application and prescribed burning, are presently used on brush-dominated rangelands in the cross timbers of Oklahoma to improve livestock grazing potential (Engle, 1987). The cross timbers vegetation type supports a wide variety of small mammal species and the impact of such range modifications on cuterebrid infections in this host community is currently unknown. The objective of my study was to examine the influence of these habitat modifications on cuterebrid parasitism in small mammal communities of central Oklahoma. I specifically wanted to test the hypotheses that alterations of structural components of habitats required by cuterebrids influences the degree of parasitism among hosts, and the degree of parasitism among populations whithin a host community are correlated.

MATERIALS AND METHODS

Study area

Rodents and cottontail rabbits (Sylvilagus floridanus) were collected on the Cross Timbers Experimental Range (CTER) which is located approximately 11 km west of Stillwater, Oklahoma in Payne County. 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 x 0.83 km) fenced experimental pastures, representing 4 replications of 4 brush management treatments, using combinations of herbicide and annual prescribed burning applications, and an untreated control (Appendix D). This provides a 2 x 2 factorial experimental design of 4 replications of 5 treatments. The 5 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) 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) applied aerially at 2.2 kg per ha in June 1983; (4) triclopyr applied (as with #3) with annual prescribed burning in April, beginning in 1985; (5) untreated control. All experimental pastures were moderately grazed by cattle throughout spring and summer of each year.

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 by understory woody species reduced the production of herbaceous plants after the triclopyr treatment.

Data collection

Collection of rodents occurred from July to September (summer) and December to March (winter) from 1986- 1988. Sampling was conducted by removal snap-trapping using a randomly placed 8 X 8 transect grid with 15 meter spacing between trap stations within each pasture. Snap traps were baited with peanut butter-rolled oats mixture and apples for 3 consecutive days. Cottontail rabbits were collected in January (winter) and July (summer) of 1987 and 1988. An attempt was made to collect 5 cottontail rabbits (Sylvilagus floridanus) from each of 2 replications for the 5 experimental treatments resulting in 50 samples per season. Host specimens were frozen immediately after collection then necropsied and eviscerated as time allowed. Ages of rodents were based on body weight; white-footed mouse (Peromyscus leucopus), adult ≥ 19.0 g; eastern woodrat (Neotoma floridana), adult ≥ 200.0 g, fulvous harvest mouse (Reithrodontomys fulvescens), adult ≥ 10.0 g. Ages of cottontail rabbits were determined using a combination of reproductive status and body weight where animals ≥800 g body weight or reproductively active between 650 and 799 g were considered adults. No analyses of data were performed for animals collected in winter due to a scarcity of infections. Low prevalences of Cuterabra sp. infection among cottontail rabbit (n = 14) and fulvous harvest mouse (n = 2) populations precluded analysis of year, brush treatment, host age, and sex effects. A representative sample of Cuterebra sp. recovered from this study has been deposited in the U. S. National Parasite Collection, Beltsville, Maryland 20705, U.S.A. (Accession no. 80571).

Data analysis

The terms intensity and prevalence are defined by Margolis et al. (1982). The main and interactive effects of year, treatment, host sex, and age were examined with a factorial analysis of variance for the intensity of recovered Cuterebra sp. (PROC GLM, SAS, Statistical Analysis Systems, SAS Institute, Raleigh, North Carolina). Protected multiple comparisons (LSD) were used when significant differences ($P \leq 0.100$) were detected by analysis of variance. Prevalence was subjected to chi-square analysis for determination of heterogeneity between years, brush treatments, host sex, and age. Relationships of prevalence of Cuterebra sp. with host density and among host species within the small mammal community were examined using Spearman correlation analysis (PROC CORR, SAS). Copies of raw data and statistical analyses are available upon request from Robert L. Lochmiller.

RESULTS

Prevalence

Of the 10 species of small mammals collected on the CTER from 1986 through 1988, 6 species, silky pocket mouse (Perognathus flavous), pine vole (Microtus pineatorum), least shrew (Cryptotis parva), short-tailed shrew (Blarina brevicauda), cotton rat (Sigmodon hispidus), and house mouse (Mus musculus) did not have representative infections of Cuterebra sp. These species were not included in data analysis, resulting in a data set of 811 small mammals in the host community; white-footed mouse (n = 444), eastern woodrat (n = 231), fulvous harvest mouse (n = 36), and cottontail rabbit (n = 100).

Prevalence of Cuterebra sp. infection within the host community (19.4%) differed ($P < 0.001$) among years, (all treatments pooled) and host species (all years pooled, $P < 0.010$). No significant differences (all years pooled, $P > 0.100$) were indicated among brush treatments (Table 1), or host sexes and ages (Table 2). Prevalence was highest in 1987 (37.8%) and lowest in 1986 (7.9%). Prevalences of Cuterebra sp. infection in host communities in 1986 (n =

380) were not significantly affected (all treatments pooled, P $\geq$ 0.250) by host species, sex, or age. However, prevalence of Cuterebra sp. infection was significantly (P < 0.025) greater in small mammals from unburned (13.4%) than burned pastures (6.1%) and greater (P < 0.100) in tebuthiuron (14.7%) than tricolpyr-treated pastures (8.7%) in 1986. Prevalences of Cuterebra sp. infection in host communities in 1987 (n = 231) and 1988 (n = 200) were significantly influenced by differences among host species (P $\leq$ 0.100) but not sex (P > 0.100) or brush treatment. There was no correlation (P > 0.400) between prevalence of Cuterebra sp. and density (animals/100 trap nights) of host communities.

Prevalence of Cuterebra sp. infection in eastern woodrat populations differed significantly (P < 0.001) among years of collection and was greater (P < 0.025) on unburned pastures (10.9%) compared to burned treatments (0%) in 1986 (n = 64). Prevalence of Cuterebra sp. infections in 1987 (n = 85) was significantly (P < 0.100) greater in eastern woodrat populations inhabiting pastures treated with triclopyr (42.6%) than those from tebuthiuron-treated pastures (16.7%). Prevalence of Cuterebra sp. infection in 1988 (n = 82) was greater (P < 0.100) in females (32.4%) than males (16.7%) and greater (P < 0.005) in adults (71.4%) than juveniles (23.0%). Prevalences of Cuterebra sp. infections were not different (P > 0.100) among host sexes or ages in 1986 and 1987, or brush treatments in 1988.

Prevalence of Cuterebra sp. infections in white-footed mouse populations from 1986 to 1988 (18.5%) was greater (P < 0.050) in tebuthiuron (27.2%) than triclopyr-treated pastures (13.8%) but differed (P < 0.001) among years of collection. Prevalence of Cuterebra sp. infections in 1986 (n = 298) was greater (P < 0.100) in white-footed mouse populations inhabiting pastures treated with tebuthiuron (15.4%) than triclopyr (7.9%). Prevalence of Cuterebra sp. infection in 1987 (n = 88) was greater (P < 0.001) in white-footed mouse populations from burned (71.4%) than unburned (44.2%) pastures. Prevalence of Cuterebra sp. infections was greater (P < 0.025) in juveniles (14.6%) than adults (5.6%) in 1986 and greater (P < 0.005) in adults (38.9%) than juveniles (0%) in 1988. No significant (P > 0.100) differences in Cuterebra sp. infection were found between adult and juvenile white-footed mice in 1987 or between sexes throughout the study.

Prevalence of Cuterebra sp. infection in cottontail rabbit and fulvous harvest mouse populations from 1986 to 1988 was 14.0% and 5.6% respectively. Warbles in eastern woodrats and cottontail rabbits were typically (93.2%) located on the throat while those in white-footed mice were typically (97.6%) located in the groin (Table 3).

Intensity

Overall intensity of Cuterebra sp. infection in the host community averaged 1.33 ± 0.05 warbles/infected host (ranged from 1 to 5) and was significantly ($P < 0.022$) different among years of collection and host species ($P < 0.021$). Intensity of infection was highest in 1987 (1.46 ± 0.09) and lowest in 1986 (1.10 ± 0.06). No significant differences were found due to brush treatment ($P > 0.500$), host sex ($P > 0.626$) or age ($P > 0.371$). Intensities of Cuterebra sp. infection in 1986 and 1988 were not significantly ($P > 0.237$) different among host species, sexes, ages or brush treatments. Intensity of Cuterebra sp. infection in 1987 differed ($P < 0.061$) among host species but not ($P > 0.100$) between host sex, age or brush treatments.

Mean intensities of Cuterebra sp. infection in eastern woodrats (1.54 ± 0.11), white-footed mice (1.21 ± 0.05), fulvous harvest mice (1.00 ± 0), and cottontail rabbits (1.21 ± 0.11) were not significantly ($P > 0.100$) affected by brush treatment, host sex, or age during any year of collection.

DISCUSSION

Prevalence of Cuterebra sp. infection from my study was lower than previously reported surveys for white-footed mice from Virginia (Hensley, 1976) and Iowa (Dalmat, 1943) while prevalence in woodrats was greater than those reported from Kansas (Beamer et al., 1943). Cottontail rabbit populations in my study had lower prevalences of Cuterebra sp. infection than those from Virginia (Jacobson et al., 1978) and Wisconsin (Hass and Dicke, 1958). Location of warbles on hosts from my study were in general agreement with previous reports regarding Cuterebra sp. parasitism in white-footed mice, woodrats and cottontail rabbits (Beamer et al., 1943; Catts, 1965; Hass and Dicke, 1958; Hensley, 1976; Baird, 1979). There is a great deal of variability in information regarding prevalence among sex and age classes of small mammals (Catts, 1965; Hensley, 1976). Although Cuterebra sp. prevalence among white-footed mice and eastern woodrats was intermittently influenced by host sex and age, our results did not indicate that these were consistent factors in the distribution of Cuterebra sp. parasitism in the host community on the CTER.

My results indicated that Cuterebra sp. parasitism was independent of host density and supported previous research which demonstrated that host density is not an important factor (Bennett, 1972). Jacobson et al. (1978) suggested that environmental factors and meterologic conditions were responsible for the lack of correlation between host density and C. buccata parasitism in cottontail rabbits.

Bennett (1972) speculated that habitat preferences by adult female bot flies may be very important in determining Cuterebra sp. distribution. Previous studies (Catts, 1967; Hunter, 1973) have reported that aggregations of Cuterebra sp. are associated with sunny locations near topographic summits ssuch as tall trees on sunny hillsides. Gravid females leave these areas after mating to search for host habitat on which to oviposit. This information would suggest that Cuterebra sp. infection could be limited more by optimal bot fly aggregation sites than host age, sex, behavior, or density factors. This appears to be true on the CTER. Tebuthiuron-treated pastures provide an open canopy with abundant topographic summits (snags and eastern redcedar trees) but supported lower densities of white-footed mice and eastern woodrats (83% of the host community) than triclopyr-treated pastures. Greater prevalence of Cuterebra sp. infection in the host community from unburned pastures compared to burned pastures could be associated with death of fossorial larvae due to high soil temperatures during the burn and post-burn changes in microclimate which can result from elimination of litter and accumulation of ash (Ewing and Engle, 1988).

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Table 1. Prevalence (number infected/number examined) of Cuterebra sp. infection in 3 species of small mammals and 1 species of cottontail rabbit collected from 5 experimental brush treatments on the Cross Timbers Experimental Range, Payne County, Oklahoma, in summers of 1986, 1987, and 1988.

	Brush treatment					
Host species	Tebuthiuron	Tebuthiuron and burn	Triclopyr	Triclopyr and burn	Control	Total
1986						
Neotoma floridana	1/7	0/5	5/22	0/24	1/6	7/64
Peromyscus leucopus	10/51	6/43	10/84	3/81	2/39	31/298
Reithrodontomys fulvescens	0/5	0/5	0/2	1/6	NC	1/18
Total	11/62	6/51	15/108	4/111	3/45	39/380
1987						
Neotoma floridana	2/7	0/5	13/33	16/35	2/5	33/85
Peromyscus leucopus	4/20	12/17	3/14	13/18	12/19	44/88
Reithrodontomys fulvescens	0/2	0/3	NC	1/3	NC	1/8
Sylvilagus floridanus	2/10	3/10	0/10	3/10	1/10	9/50
Total	8/39	15/35	16/57	22/66	15/34	86/231
1988						
Neotoma floridana	3/9	4/12	6/24	4/29	2/8	19/82
Peromyscus leucopus	1/8	1/4	1/12	0/8	4/16	7/58
Reithrodontomys fulvescens	0/3	0/3	NC	0/2	NC	0/10
Syvilagus floridanus	3/10	0/10	0/10	1/10	1/10	5/50
Total	7/30	5/41	7/46	5/49	7/34	31/200
Overall prevalence	26/131	26/127	38/211	31/226	25/113	157/811

NC = No capture

Table 2. Prevalence (number infected/number examined) of <u>Cuterebra</u> sp. infection among small mammals and cottontail rabbits across age and sex categories. Host species were collected from the Cross Timbers Experimental Range, Payne County, Oklahoma in summer 1986, 1987, and 1988.

Host species		Host age		
		Adult	Juvenile	Total
<u>Neotoma floridana</u>				
	Male	15/51	13/73	28/124
	Female	9/37	22/70	31/107
	Total	24/88	25/143	59/231
<u>Peromyscus leucopus</u>				
	Male	25/111	16/126	41/237
	Female	21/115	20/92	41/207
	Total	46/226	36/218	82/444
<u>Riethrodontomys fulvescens</u>				
	Male	2/20	0/3	2/23
	Female	0/11	0/2	0/13
	Total	2/31	0/5	22/36
<u>Sylvilagus floridanus</u>				
	Male	6/36	2/9	8/45
	Female	5/39	1/16	6/55
	Total	11/75	3/25	14/100
	Overall total	83/420	74/391	157/811

Table 3. Location of *Cuterebra* sp. warbles on male and female small mammals and cottontail rabbits collected from the Cross Timbers Experimental Range, Payne County, Oklahoma in summer 1986, 1987, 1988.

	Location of warble				
Host species	Inguinal	Scrotal	Throat	Other	Total
Neotoma floridana					
Male	0	1	26	1	28
Female	1	NA	30	0	31
Total	1	1	56	1	59
Peromyscus leucopus					
Male	26	15	0	1	42
Female	39	NA	1	0	40
Total	65	15	1	0	82
Reithrodontomys fulvescens					
Male	1	0	0	1	2
Female	NA	NA	NA	NA	NA
Total	1	0	0	1	2
Sylvilagus floridanus					
Male	1	0	8	0	9
Female	1	0	4	0	5
Total	2	0	12	0	14

NA = Not applicable

APPENDIXES

APPENDIX A

HELMINTHS RECOVERED FROM COTTONTAIL RABBITS (SYLVILAGUS FLORIDANUS) AT THE CROSS TIMBERS EXPERIMENTAL RANGE

Key to abbreviations:

OC = Obeliscoides cuniculi
TC = Trichostrongylus calcaratus
PN = Passalurus nonannulatus
DV = Dermatoxys veligera
WL = Wellcomia longejector
TP = Taenia pisiformis
MP = Mosgovoyia pectinata

A = Adult
J = Juvenile
P = Pregnant
L = Lactating
N = Neutral/ non-scrotal testis
S = Scrotal testis

Ind.	Trt.	Seas./ Yr.	Age	Sex	Repr. Cond.	OC	TC	PN	DV	WL	TP	MP
52	4	W/87	A	F	N	000	144	120	0	0	0	0
53	4	W/87	A	F	N	1	528	0	0	0	0	0
54	4	W/87	A	M	N	14	936	0	0	0	5	1
57	5	W/87	A	M	N	55	8	0	20	0	14	2
58	5	W/87	A	F	N	118	1512	10	0	0	8	1
59	1	W/87	A	M	N	14	560	0	0	0	15	0
60	5	W/87	A	M	N	14	416	10	0	0	6	1
62	1	W/87	A	F	N	4	580	370	0	0	0	0
63	5	W/87	A	F	N	52	316	60	0	0	20	1
64	4	W/87	A	F	N	5	60	0	0	0	2	0
65	4	W/87	A	F	N	3	236	0	0	0	16	0
66	4	W/87	A	M	N	8	56	10	0	0	2	1
67	4	W/87	A	M	N	14	488	0	0	0	1	0
68	4	W/87	A	F	N	7	148	50	0	0	27	0
69	5	W/87	A	F	N	6	36	0	0	0	0	0
70	3	W/87	A	M	N	4	1084	770	0	0	13	1
71	5	W/87	A	M	N	17	112	0	0	0	1	2
72	2	W/87	A	M	N	25	276	0	0	0	2	4
73	2	W/87	A	M	N	4	720	0	10	0	2	1
74	3	W/87	A	F	N	7	156	0	0	0	1	1
75	3	W/87	J	M	N	36	1308	0	40	0	0	1
76	5	W/87	A	F	N	58	528	0	0	0	5	1
77	5	W/87	A	M	N	42	488	0	0	0	7	1
78	5	W/87	A	F	N	0	188	150	0	0	13	1
79	5	W/87	A	F	N	1	12	2760	0	0	8	2

Ind.	Trt.	Seas./ Yr.	Age	Sex	Repr. Cond.	OC	TC	PN	DV	WL	TP	MP
80	3	W/87	A	F	N	20	180	0	0	0	2	1
81	3	W/87	A	M	N	25	96	0	0	0	0	1
82	4	W/87	A	F	N	26	956	3160	0	0	5	1
83	4	W/87	A	F	N	10	0	70	0	0	7	0
84	1	W/87	A	M	N	1	128	0	0	0	1	0
85	1	W/87	A	F	P	9	228	0	0	0	4	1
86	1	W/87	A	F	N	17	128	0	0	0	7	1
87	1	W/87	A	F	P	3	304	0	0	0	4	1
88	1	W/87	A	M	N	13	248	0	0	0	2	0
89	1	W/87	A	M	N	36	160	0	0	0	11	1
90	1	W/87	A	F	N	1	620	0	0	0	4	1
91	1	W/87	A	F	P	5	44	0	0	0	6	0
92	2	W/87	A	F	N	34	128	0	0	0	1	1
93	2	W/87	A	F	N	0	536	0	0	0	13	0
94	2	W/87	A	M	N	15	420	0	0	0	11	2
95	2	W/87	A	M	N	102	728	0	0	0	9	1
96	2	W/87	A	F	N	6	44	0	0	0	5	0
97	2	W/87	A	F	N	7	536	0	10	0	6	0
98	2	W/87	A	F	N	20	216	0	0	0	0	0
99	2	W/87	A	M	N	113	264	340	0	0	6	1
100	3	W/87	A	M	N	331	356	1840	0	0	1	1
101	3	W/87	A	M	N	41	492	0	0	0	20	0
102	3	W/87	A	M	N	66	552	0	0	0	0	1
103	3	W/87	A	F	P	13	88	0	0	0	2	0
104	2	W/87	A	M	N	215	568	1300	0	0	1	1
105	3	W/87	A	F	N	5	184	0	0	0	0	1
106	3	S/87	A	M	S	165	148	80	240	0	4	3
107	3	S/87	A	F	PL	26	164	3250	50	0	0	6
108	3	S/87	J	F	N	5	12	30	0	0	0	2
109	3	S/87	A	M	S	4	0	0	50	0	15	22
110	3	S/87	J	M	N	104	332	10	0	0	0	0
111	3	S/87	A	M	S	111	56	0	50	0	0	1
112	4	S/87	A	M	S	4	0	0	0	0	12	0
113	4	S/87	A	F	L	9	20	0	0	0	5	1
114	2	S/87	A	M	S	13	72	0	40	0	10	1
115	2	S/87	A	M	S	31	8	0	0	0	5	0
116	2	S/87	A	F	L	77	144	0	20	0	15	1
117	1	S/87	A	M	S	19	64	10	0	0	0	1
118	1	S/87	A	M	S	62	132	0	0	0	0	1
119	1	S/87	A	M	S	50	36	0	0	0	2	1
120	1	S/87	J	F	N	3	12	0	0	0	0	0
121	4	S/87	J	M	N	70	36	0	0	0	0	5
122	4	S/87	J	F	N	83	172	0	0	0	0	1
123	2	S/87	A	M	S	67	24	30	30	0	16	1
124	5	S/87	A	F	L	184	168	0	0	0	14	6
125	5	S/87	A	M	S	39	80	150	0	0	0	2

Ind.	Trt.	Seas./ Yr.	Age	Sex	Repr. Cond.	OC	TC	PN	DV	WL	TP	MP
126	5	S/87	A	M	S	77	164	0	0	0	0	5
127	1	S/87	A	F	P	13	236	0	20	0	0	1
128	1	S/87	A	F	P	15	8	0	10	0	111	0
129	4	S/87	A	M	S	102	136	0	0	0	12	5
130	2	S/87	A	F	P	18	44	790	0	50	15	6
131	2	S/87	A	F	L	63	92	0	10	0	13	23
132	5	S/87	J	F	N	40	20	0	0	0	0	9
134	5	S/87	J	M	N	13	4	0	0	0	0	3
135	5	S/87	A	F	N	24	36	20	30	0	0	1
136	3	S/87	A	M	N	53	28	0	0	0	0	2
137	1	S/87	A	F	L	158	60	170	0	0	158	1
138	1	S/87	A	F	N	76	100	0	0	0	11	7
139	3	S/87	A	F	PL	81	8	20	0	0	2	4
140	4	S/87	A	F	L	98	1072	10	0	0	1	3
141	4	S/87	A	F	P	6	132	0	0	0	7	13
142	2	S/87	A	M	S	115	1220	8720	0	100	2	7
143	2	S/87	A	M	S	31	4	0	40	0	0	0
144	2	S/87	J	M	N	101	328	0	0	0	7	1
145	2	S/87	A	F	L	84	92	0	0	0	15	2
146	3	S/87	A	F	L	39	288	0	0	0	17	3
147	5	S/87	J	F	N	25	48	10	0	0	0	2
148	1	S/87	A	M	S	11	44	520	0	0	32	3
149	1	S/87	A	F	L	86	132	10	0	0	1	12
150	5	S/87	A	M	S	26	88	0	0	0	8	0
151	5	S/87	J	F	N	36	148	20	0	0	12	5
152	4	S/87	J	F	N	36	380	5590	0	0	0	4
153	4	S/87	J	F	N	94	452	0	0	0	15	7
154	3	S/87	A	M	S	44	80	0	40	0	14	6
155	4	S/87	J	M	N	82	384	0	0	0	0	0
156	5	S/87	A	M	S	15	4	0	10	0	2	0
157	5	S/87	A	M	S	66	84	10	0	0	1	5
158	3	W/88	A	F	N	5						
159	3	W/88	A	M	N	1						
160	5	W/88	A	F	N	0						
161	5	W/88	A	M	N	1						
162	5	W/88	A	M	S	1						
163	5	W/88	A	F	N	3						
164	4	W/88	A	M	S	2						
165	2	W/88	A	M	S	2						
166	2	W/88	A	M	S	3						
167	2	W/88	A	F	N	1						
168	1	W/88	A	F	N	11						
169	4	W/88	A	F	N	7						
170	5	W/88	A	F	N	7						
171	5	W/88	A	M	S	1						
172	1	W/88	A	M	N	2						
173	3	W/88	A	M	S	3						
174	3	W/88	A	F	N	3						

Ind.	Trt.	Seas./ Yr.	Age	Sex	Repr. Cond.	OC
175	5	W/88	A	F	N	12
176	2	W/88	A	F	N	8
177	2	W/88	A	F	N	10
178	3	W/88	A	M	S	4
179	3	W/88	A	M	S	33
180	2	W/88	A	M	S	0
181	4	W/88	A	F	N	10
182	3	W/88	A	M	S	20
183	3	W/88	A	F	N	6
184	5	W/88	A	F	N	3
185	4	W/88	A	M	S	4
186	5	W/88	A	F	N	1
187	5	W/88	A	F	N	11
188	4	W/88	A	F	N	2
189	2	W/88	A	F	N	9
190	2	W/88	A	M	S	13
191	1	W/88	A	F	N	48
192	1	W/88	A	M	S	4
193	4	W/88	A	F	N	4
194	4	W/88	A	M	N	11
195	4	W/88	A	M	S	4
196	3	W/88	A	F	N	17
197	4	W/88	A	F	N	12
198	4	W/88	A	M	S	54
199	1	W/88	A	F	P	5
200	1	W/88	A	F	N	6
201	2	W/88	A	M	S	13
202	3	W/88	A	M	S	12
203	2	W/88	A	F	N	23
204	1	W/88	A	M	S	10
205	1	W/88	A	M	S	86
206	1	W/88	A	M	S	69
207	1	W/88	A	F	N	34
208	1	W/88	A	M	S	108
209	1	W/88	A	M	S	41
210	1	W/88	A	M	S	11
211	2	S/88	A	F	N	32
212	2	S/88	A	M	S	7
213	2	S/88	A	M	S	32
214	2	S/88	A	F	N	51
215	2	S/88	J	M	N	67
216	4	S/88	A	M	S	24
217	4	S/88	A	M	S	7
218	4	S/88	A	M	S	12
219	4	S/88	A	M	S	36
220	4	S/88	A	M	S	78
221	2	S/88	A	M	S	15

Ind.	Trt.	Seas./ Yr.	Age	Sex	Repr. Cond.	OC
222	2	S/88	A	F	L	149
223	2	S/88	A	F	N	435
224	2	S/88	A	F	PL	41
225	2	S/88	A	F	PL	53
227	1	S/88	A	M	S	70
228	1	S/88	A	M	S	83
229	1	S/88	J	F	N	63
230	1	S/88	A	F	N	84
231	1	S/88	A	F	L	92
232	4	S/88	A	F	PL	36
233	4	S/88	J	M	N	73
234	1	S/88	J	F	N	32
235	3	S/88	A	F	N	22
236	3	S/88	A	M	S	24
237	5	S/88	A	F	N	15
238	5	S/88	A	F	N	10
239	5	S/88	A	F	L	15
240	3	S/88	A	M	S	20
241	3	S/88	A	M	S	68
242	3	S/88	A	M	S	122
243	5	S/88	A	F	N	78
244	5	S/88	A	F	N	46
245	5	S/88	A	M	S	17
246	5	S/88	A	F	P	133
247	1	S/88	A	F	N	10
248	1	S/88	A	F	L	7
249	1	S/88	A	F	P	37
250	1	S/88	J	M	N	1
251	5	S/88	A	F	L	166
252	5	S/88	A	M	S	80
253	3	S/88	J	F	N	111
254	3	S/88	J	F	N	41
255	3	S/88	J	F	N	31
256	3	S/88	J	F	N	119
257	4	S/88	J	M	N	77
258	5	S/88	A	M	S	64
259	4	S/88	A	F	L	38
260	4	S/88	J	F	N	97

APPENDIX B

HELMINTHS RECOVERED FROM COTTON RATS (SIGMODON HISPIDUS) AT THE CROSS TIMBERS EXPERIMENTAL RANGE, PAYNE COUNTY, OKLAHOMA

Key to abbreviations:

LA = Longistriata adunca
SS = Strongyloides sp.
SY = Syphacia sigmodontis
RA = Raillietina sp.
PM = Protospirura muris

Individual	**Treatment**	**Sex**	**Season**	**LA**	**SS**	**SY**	**RA**	**PM**
52	1	F	W	134	12	0	3	0
87	1	M	W	150	0	0	0	0
88	1	M	W	320	0	0	0	0
133	1	M	W	52	34	0	1	0
134	1	F	W	46	0	0	6	0
135	1	M	W	18	0	0	1	0
135	1	M	W	244	2	0	0	0
160	1	F	W	2	0	0	1	0
161	1	F	W	60	0	0	1	0
164	1	F	W	108	0	0	0	0
113	2	F	W	40	0	0	0	0
114	2	F	W	282	0	0	0	0
115	2	M	W	460	30	0	0	0
120	2	M	W	60	10	0	0	0
121	2	M	W	394	4	0	0	0
122	2	M	W	144	0	0	0	0
124	2	F	W	10	0	0	1	0
125	2	F	W	0	12	0	1	0
166	2	F	W	244	2	0	0	0
167	2	M	W	0	10	0	0	0
3057	2	M	W	80	0	0	0	0
3123	2	M	W	610	0	0	0	0
3129	2	M	W	30	0	0	0	0
30	3	F	W	120	0	0	0	0
31	3	F	W	40	0	0	0	0

Individual	Treatment	Sex	Season	LA	SS	SY	RA	PM
32	3	F	W	110	1	0	0	0
34	3	F	W	0	0	0	0	0
37	3	M	W	286	0	2	0	0
94	3	M	W	152	4	36	1	0
95	3	M	W	166	14	0	0	0
96	3	F	W	250	20	0	2	0
98	3	M	W	64	0	0	0	0
106	3	M	W	130	0	0	0	0
3028	3	M	W	320	0	0	0	0
3029	3	M	W	520	0	0	0	0
3036	3	M	W	70	0	0	0	0
3102	3	M	W	240	0	0	0	0
3103	3	M	W	30	0	20	0	0
61	4	M	W	490	2	0	0	0
62	4	F	W	350	0	0	0	0
64	4	F	W	150	0	0	0	0
65	4	M	W	90	0	0	0	0
66	4	M	W	230	10	0	0	0
68	4	F	W	396	0	0	0	0
69	4	F	W	572	0	0	0	0
70	4	F	W	590	0	0	0	0
138	4	M	W	198	2	0	0	0
155	4	M	W	180	0	0	1	0
3060	4	M	W	180	0	0	0	0
3063	4	M	W	600	0	0	0	0
901	5	F	W	28	2	2302	1	3
902	5	M	W	12	0	8	4	4
903	5	M	W	14	0	132	1	1
904	5	F	W	0	0	96	0	0
905	5	M	W	2	0	0	0	7
906	5	M	W	14	0	0	1	0
907	5	F	W	18	0	0	1	0
908	5	M	W	92	0	294	0	6
1033	1	F	S	190	0	0	2	0
1049	1	F	S	202	2	0	13	0
1051	1	M	S	618	10	0	1	0
1071	1	F	S	14	2	72	7	0
1074	1	M	S	82	0	264	3	0
1079	1	F	S	0	40	0	0	0
1083	1	M	S	0	0	0	0	0
1095	1	F	S	22	0	0	2	0
1111	1	M	S	216	0	0	0	0
1125	1	M	S	120	0	0	0	0
4034	1	M	S	1090	0	150	2	0
4057	1	M	S	259	0	0	0	0
1001	2	F	S	74	0	0	0	0
1002	2	M	S	40	0	0	0	0

Individual	Treatment	Sex	Season	LA	SS	SY	RA	PM
1003	2	M	S	110	0	0	0	0
1004	2	M	S	0	0	0	0	0
1006	2	M	S	60	0	10	0	0
1021	2	M	S	110	0	0	0	0
1026	2	F	S	30	0	0	0	0
1046	2	F	S	114	0	32	0	0
1062	2	F	S	208	4	4004	0	0
1063	2	F	S	66	0	0	0	0
4060	2	M	S	663	0	0	0	0
4061	2	M	S	450	0	0	0	0
1032	3	M	S	132	0	0	0	0
1047	3	M	S	540	30	0	1	0
1070	3	F	S	114	0	0	1	0
1093	3	M	S	100	20	0	0	0
1094	3	F	S	310	0	0	1	0
1100	3	F	S	380	30	1510	0	0
1106	3	F	S	0	0	0	0	0
1110	3	M	S	314	4	6328	0	0
1112	3	M	S	2	0	0	0	0
2095	3	M	S	172	0	102	0	0
3028	3	M	S	320	0	0	0	0
3029	3	M	S	520	0	0	0	0
3036	3	M	S	70	0	0	0	0
3102	3	M	S	240	0	0	0	0
3103	3	M	S	30	0	20	0	0
4096	3	M	S	340	0	0	0	0
4102	3	M	S	150	0	0	0	0
4103	3	M	S	140	0	0	0	0
4108	3	M	S	2110	0	210	0	0
4111	3	M	S	1030	0	0	0	0
1010	4	M	S	20	20	0	0	0
1018	4	M	S	110	0	0	0	0
1034	4	F	S	12	0	0	0	0
1035	4	F	S	464	0	0	5	0
1038	4	F	S	722	30	0	0	0
1075	4	M	S	20	0	0	0	0
1082	4	M	S	240	40	0	2	0
1174	4	M	S	80	0	0	0	0
2032	4	F	S	316	0	0	1	0
2110	4	F	S	76	0	0	0	0
4017	4	M	S	40	0	0	0	0
1091	5	F	S	1014	0	0	1	0
1092	5	F	S	448	0	0	0	0
1193	5	M	S	558	0	0	1	0
1094	5	M	S	386	0	0	0	0
2035	5	F	s	308	0	36	0	0

APPENDIX C

HELMINTHS RECOVERED FROM EASTERN WOODRATS (NEOTOMA FLORIDANA) COLLECTED AT THE CROSS TIMBERS EXPERIMENTAL RANGE

Key to abbreviations:

BW = Bohmiella wilsoni
LN = Longistriata neotomae
TM = Trichuris muris

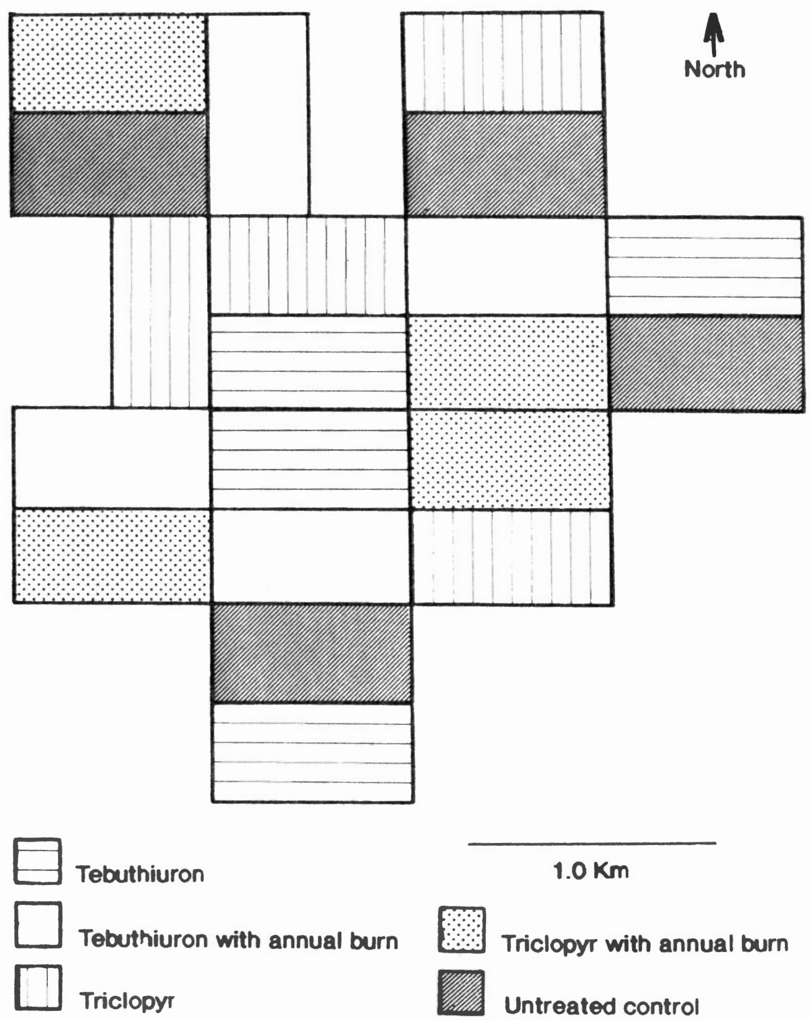
Individual	Treatment	Sex	Season	BW	LN	TM
0012	1	F	W	12	20	0
0015	1	M	W	4	90	0
0018	1	M	W	3	30	2
0019	1	F	W	9	20	0
0020	1	M	W	0	120	0
0101	1	M	W	0	0	0
0102	1	F	W	0	20	0
0201	1	F	W	0	70	0
0207	1	M	W	11	8	32
0208	1	F	W	10	192	0
0009	2	F	W	0	40	1
0010	2	F	W	7	60	0
0011	2	M	W	3	0	2
0014	2	M	W	0	0	1
0106	2	M	W	0	0	0
0211	2	F	W	3	0	0
0217	2	F	W	6	4	0
0001	3	M	W	0	70	0
0006	3	F	W	33	0	0
0008	3	M	W	10	30	2
0105	3	M	W	18	0	0
0107	3	F	W	0	0	0
0109	3	M	W	5	0	0
0110	3	F	W	15	0	0
0111	3	M	W	1	0	4
0112	3	M	W	18	0	0
0113	3	M	W	0	8	0
0210	3	F	W	7	16	2
0218	3	F	W	19	4	2

Individual	Treatment	Sex	Season	BW	LN	TM
0016	4	M	W	3	50	4
0017	4	F	W	110	0	0
0114	4	M	W	23	0	6
0115	4	M	W	17	0	0
0301	4	M	W	2	60	2
0202	4	F	W	26	196	20
0203	4	F	W	14	30	0
0204	4	F	W	0	4	0
0205	4	F	W	19	32	6
0206	4	F	W	9	0	1
0005	5	M	W	18	1350	0
0007	5	M	W	10	160	1
0104	5	M	W	64	36	22
0204	5	F	W	0	50	0
0042	1	F	S	9	120	0
0051	1	M	S	0	40	0
0053	1	M	S	0	40	0
0101	1	F	S	0	22	1
0105	1	F	S	0	54	0
0106	1	F	S	0	12	0
0233	1	M	S	1	50	0
0251	1	F	S	82	0	0
0225	1	M	S	1	42	0
0001	2	M	S	0	60	0
0015	2	F	S	3	0	0
0049	2	F	S	14	90	0
0107	2	M	S	4	4	0
0224	2	F	S	0	10	4
0313	2	F	S	0	56	0
0318	2	F	S	0	120	0
0319	2	M	S	0	234	0
0320	2	F	S	0	62	0
0024	3	F	S	0	4	0
0025	3	F	S	0	100	0
0026	3	F	S	5	90	0
0027	3	F	S	4	50	0
0028	3	M	S	0	0	0
0032	3	F	S	4	0	0
0033	3	F	S	4	130	0
0034	3	F	S	0	40	0
0035	3	F	S	0	30	0
0039	3	M	S	1	60	0
0041	3	F	S	0	90	0
0044	3	F	S	19	50	0
0045	3	F	S	0	100	0
0215	3	F	S	1	52	0
0217	3	F	S	0	52	0

Individual	Treatment	Sex	Season	BM	LN	TM
0003	4	M	S	0	20	0
0004	4	F	S	16	0	0
0005	4	M	S	0	0	0
0007	4	F	S	0	0	0
0018	4	M	S	0	80	0
0019	4	M	S	0	30	0
0020	4	M	S	0	180	0
0021	4	F	S	0	70	0
0022	4	F	S	0	30	0
0048	4	M	S	14	30	0
0050	4	F	S	0	0	0
0212	4	F	S	3	30	2
0209	4	M	S	0	16	0
0023	5	M	S	0	60	0
0030	5	M	S	0	170	0
0031	5	M	S	9	220	0
0103	5	F	S	0	0	0
0304	5	M	S	70	152	0
0126	5	F	S	34	90	1
0164	5	M	S	0	10	0
0165	5	M	S	3	52	0

APPENDIX D

MAP OF THE CROSS TIMBERS EXPERIMENTAL RANGE, PAYNE COUNTY, OKLAHOMA.


North
Tebuthiuron
1.0 Km
Tebuthiuron with annual burn
Triclopyr with annual burn
Triclopyr
Untreated control

VITA

James F. Boggs

Candidate for the Degree of

Master of Science

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