HABITAT USE BY WHITE-TAILED DEER AND ELK ON SYMPATRIC RANGE ENZOOTIC FOR *PARELAPHOSTRONGYLUS TENUIS*

By

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Bachelor of Science

University of Massachusetts

Amherst, Massachusetts

1984

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
December, 1989

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PREFACE

Faculty and graduate students at Oklahoma State University have for many years been involved in *Parelaphostrongylus tenuis* research. Life cycle and disease aspects of *P. tenuis* have been well established in Oklahoma. However, the ecological relationships between *P. tenuis*, white-tailed deer, gastropods and abnormal hosts have not been widely studied.

The Cookson Hills Wildlife Management Area in Cherokee and Adair Counties, Oklahoma was an ideal area to begin this research. Both the elk and the deer which are sympatric on the area are surviving and providing Oklahoma sportsmen with a hunting resource. The mechanism which allows elk to survive on Cookson had not been studied and was a problem in which faculty at Oklahoma State were interested in. I would like to thank Dr. A. Alan Kocan for providing the initial idea for this research and for participating on my committee.

I wish to express my sincere appreciation to my major advisor, Dr. James H. Shaw, for his assistance during this study, for his help preparing this thesis and his support and guidance when needed.

I wish to thank Dr. David "Chip" Leslie Jr. and Dr. O.

Eugene Maughan of the Oklahoma Cooperative Fisheries and Wildlife Unit for their time, friendship and expertise.

Judy Gray and Becky Newkirk of the Oklahoma Cooperative Fisheries and Wildlife Unit deserve recognition for their time and dedication to graduate students (as long as one stays out of the office with snakes).

I wish to also thank Boyd Dill and especially Jim Boggs for the considerable amount of time they spent assisting me with this project. They spent many sleepless nights and hot days covered with chigger and tick bites. They are treasured friends.

The Oklahoma Department of Wildlife Conservation deserves thanks for allowing me full access to the Cookson Hills Wildlife Management Area. Marvin Stanley, Mike Shaw and Joe Fletcher were particularly helpful during my study.

This project would not have been possible without the financial and logistic support of the Oklahoma Cooperative Fisheries and Wildlife Unit, The Department of Zoology and Sigma Xi.

Special thanks go to my family for their encouragement and love. My wife Linda deserves my deepest appreciation for her assistance in the field, support and infinite patience throughout this long process.

This thesis is dedicated to the memory of my grandfather Joseph Adam Raskevitz (July 26, 1918 - March 3, 1987), for his consistent involvement in my education and love.

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CHAPTER I

INTRODUCTION

The nematode Parelaphostrongylus tenuis (Nematoda: Metastrongyloidea), or meningeal worm, is a neurotropic parasite that infects white-tailed deer (Odocoileus virginianus). In its normal host, white-tailed deer, P. tenuis causes little or no clinical disease. However, migration of even small numbers of P. tenuis larvae through the central nervous system of other ungulates, including desirable game species such as elk or red deer (Cervus elaphus), moose (Alces alces), caribou (Rangifer tarandus), fallow deer (Dama dama), mule and black-tailed deer (O. hemionus), results in pathologic lesions so severe that death usually results (Anderson and Prestwood 1981). In these ungulates that are considered abnormal hosts, clinical disease results from abnormal migration of P. tenuis larvae through the spinal cord of infected animals (Anderson 1985).

In infected white-tailed deer adult P. tenuis worms are usually found on cranial dura matter but also may occur in venus sinuses of the cranium. Females deposit eggs on dura matter and directly into venus sinuses. These eggs are carried to the lungs via the circulation where they are trapped in small alveolar capillaries. Eggs hatch into first stage larvae and migrate to the throat where they are swallowed and passed in the mucous coat of feces. These larvae then penetrate the foot of a terrestrial gastropod and undergo further development into infective third stage larvae. Deer become infected by ingesting infected gastropods. When eaten by a susceptible host larvae are digested out of gastropod tissue, penetrate the abomasum, and travel via lumbar nerves to the spinal cord. Larvae migrate from the lumbar region of the spinal cord to the cranium. The prepatent period is normally 82-91 days but may be longer (Fig. 1).

In abnormal hosts clinical disease is associated with the migration of P. tenuis larvae up the spinal cord. For example, in moose the larvae tend to coil upon themselves damaging the surrounding tissue. In addition, some worms remain in the spinal cord longer than normal and grow abnormally large; others travel up the central portion of the spinal cord instead of up the outside. The resulting damage to neural tissue results in symptoms such as posterior paralysis, "circling," and death (Anderson 1985).

P. tenuis is enzootic in the deciduous forest biome and the deciduous-coniferous forest ecotone of eastern North America and common as far west as Saskatchewan, Canada, and eastern Oklahoma (Anderson and Prestwood 1981, Kocan et al. 1982). Pre-colonial distribution of P. tenuis is not known. Transmission of the parasite is dependent upon availability of suitable terrestrial gastropods, which may impose a

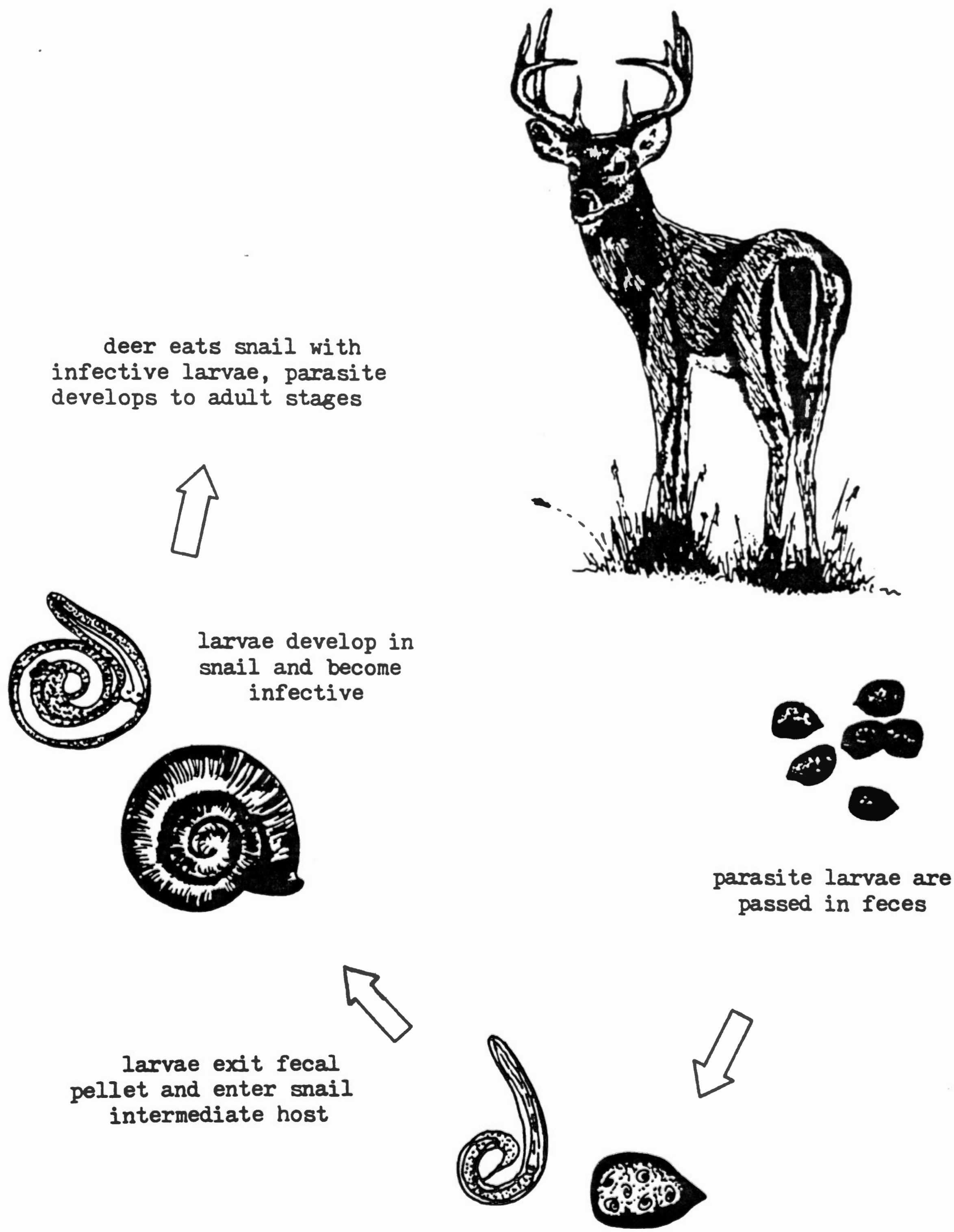

Figure 1. Life cycle of P. tenuis (From Shaw and Kocan 1982).

barrier to the spread of *P. tenuis* into areas where gastropod hosts are not found (Kocan et al. 1982).

Prior to the arrival of European man in North America, there were an estimated 10,000,000 elk of 6 subspecies that ranged from coast to coast and from Canada to Mexico. By 1922, only an estimated 90,000 elk were left; 2 subspecies were extinct, 3 were near extinction, and 1 had been extirpated from most of its original range (Bryant and Maser 1982). Since the turn of the century, conservation efforts have increased elk populations to approximately 500,000 (Bryant and Maser 1982).

Many reintroductions of elk have been attempted since the turn of the century. But reintroduction of Rocky Mountain elk (*C. e. nelsoni*) onto range formerly inhabited by the extinct eastern subspecies of elk (*C. e. canadensis*) or the extirpated Manitoban elk (*C. e. manitobensis*) have largely failed due to the susceptibility of elk to *P. tenuis* infection (Anderson and Prestwood 1981). Eveland et al. (1979) concluded that the principle limiting factor to reintroduced elk populations in Pennsylvania has been *P. tenuis*. Ecological relationships between eastern and Manitoban subspecies of elk, white-tailed deer, and *P. tenuis* are not known. Anderson (1972) suggested that either the eastern subspecies of elk was somehow resistant to infection, was able to carry the parasite without serious clinical disease, or ecological relationships between species reduced the chances of elk becoming infected. It is possible that the original range of *P*. *tenuis* was limited and allowed elk to thrive in areas free of *P*. *tenuis*, which would explain why eastern elk and Manitoban elk existed in areas now enzootic for the parasite. Severe reductions in white-tailed deer numbers around the turn of the century and subsequent restocking of *P*. *tenuis* infected deer may have been a factor in enlarging the range of *P*. *tenuis* (Kocan et al. 1982). Areas that at one time contained large herds of eastern elk or Manitoban elk may not have been enzootic for *P*. *tenuis* but are at present, thereby limiting success of many reintroductions of elk in those regions.

Between January 1969 and March 1971, the Oklahoma Department of Wildlife Conservation reintroduced 375 nonmigratory Rocky Mountain elk from the Wichita Mountains National Wildlife Refuge in southwestern Oklahoma, an area not enzootic for *P*. *tenuis* (Kocan et al. 1982) to various areas in eastern Oklahoma (Carpenter et al. 1973). As early as June 1970 an elk was observed "circling," a neurologic disturbance characteristic of *P*. *tenuis* infection near Heavener in southeastern Oklahoma. This elk later died but was never necropsied (Carpenter et al. 1973). Disease implications of *P*. *tenuis* became apparent only 18 months after reintroduction of elk to range enzootic for *P*. *tenuis* (Carpenter et al. 1973, Kocan et al. 1982) (Fig. 2).

Beginning on 15 June 1970 and continuing until 24 February 1971, elk with obvious neurologic disorders including ataxia and/or "circling" were collected from

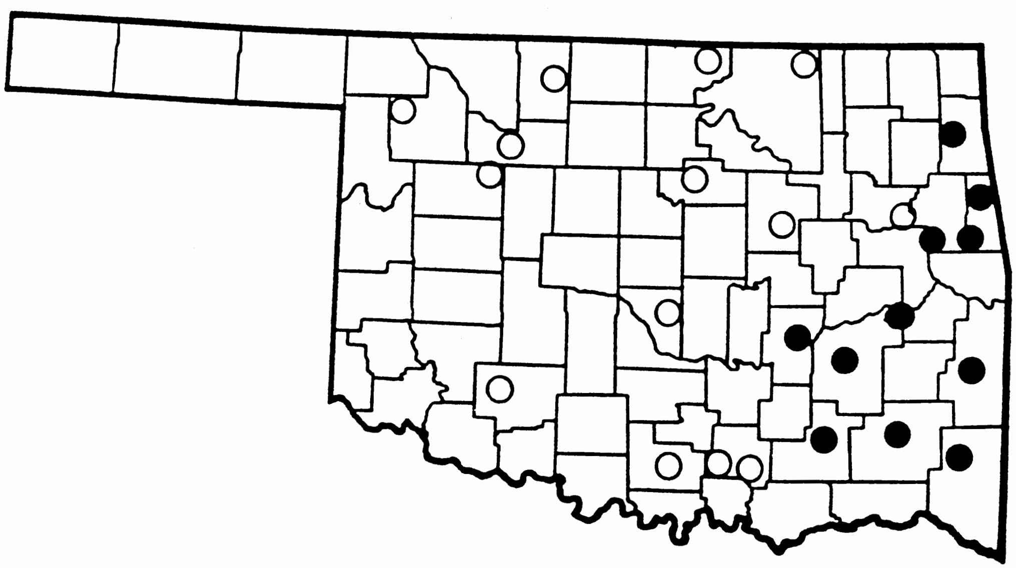

Figure 2. Distribution of _P_. _tenuis_ in Oklahoma (From Kocan et al. 1982).

Heavener and the Spavinaw Hills Wildlife Management Area. Carpenter et al. (1973) showed that clinical neurologic disease in elk reintroduced in eastern Oklahoma could be attributed directly to lesions of the central nervous system caused by *P. tenuis*, and concluded that if an area in eastern Oklahoma is to be managed primarily for elk, deer populations must be kept at a low level. However, elk populations at Cookson Hills Wildlife Management Area in eastern Oklahoma (hereafter called Cookson) are stable and are able to support a limited hunt, even in the presence of a large deer herd that was 60% infected with *P. tenuis* in 1972 (Carpenter et al. 1972) and 76% infected in 1982 (Kocan et al. 1982). The current rate of infection is between 80 and 100% (A. Kocan, Dep. Vet. Med., Okla. State Univ., pers. commun.) (Table 1).

Specific factors responsible for success of the Cookson elk herd have not been examined and the general ecological relationships between elk and white-tailed deer populations on sympatric range have not been widely studied. Relationships between moose and deer on sympatric range have been studied and tentative parallels may be drawn. Gilbert (1974) was able to show the existence of moose "refugia," or areas that were able to sustain moose populations in the presence of deer infected with *P. tenuis*. Kearney and Gilbert (1976) indicated that differential habitat use by deer and moose during spring and summer may provide the ecological habitat separation necessary to sustain moose

Table 1. Rate of *P. tenuis* infection among adult female white-tailed deer on the Cookson Hills Wildlife Management Area, 1983-1987 (From Kocan, pers. commun.).

Year	% Infection
1983	100
1984	80
1985	80
1986	100
1987	80

populations.

It is therefore possible that ecological separation of deer and elk on Cookson allows elk to persist in the presence of *P. tenuis* infected white-tailed deer. Cookson is managed to maintain large, open areas in what otherwise would be extensively forested habitat. These open areas are managed as food plots to supplement forage availability to cervids.

My objective was to determine if the success of the Cookson elk herd was related to spatial and habitat use differences between deer and elk and distribution of terrestrial gastropods. Specific objectives were: (1) evaluation of habitat use by deer and elk and (2) preliminary determination of gastropod abundance by species and habitat type.

CHAPTER II

DESCRIPTION OF STUDY AREA

My research was conducted on the Cookson Hills W.M.A. in southeastern Cherokee County and southwestern Adair County, Oklahoma (Fig. 3). Purchase of the land for the management area was authorized by the Oklahoma Fish and Game Commission in 1946. Active management principally for white-tailed deer began in 1951. More recently, the Oklahoma Department of Wildlife Conservation included Rocky Mountain elk and eastern wild turkey (*Meleagris gallopavo*) in their management objectives. Large numbers of breeding birds, game and non-game mammals, and a wide variety of herptiles also occur in Cookson.

Cookson consists of 5,456 ha of primarily rugged second-growth oak (*Quercus* spp.)-hickory (*Carya* spp.) and oak-pine (*Pinus* spp.) forest. The Cookson forest is a byproduct of the "cutout-getout," high-grade logging that existed throughout the region during the late 1800s (Savage 1976).

Savage (1976) identified 9 major habitat types on Cookson, including post oak (*Q. stellata*)-black oak (*Q. velutina*), post oak-black oak and shallow savannah range, red cedar (*Juniperus virginiana*)-hardwood and very shallow

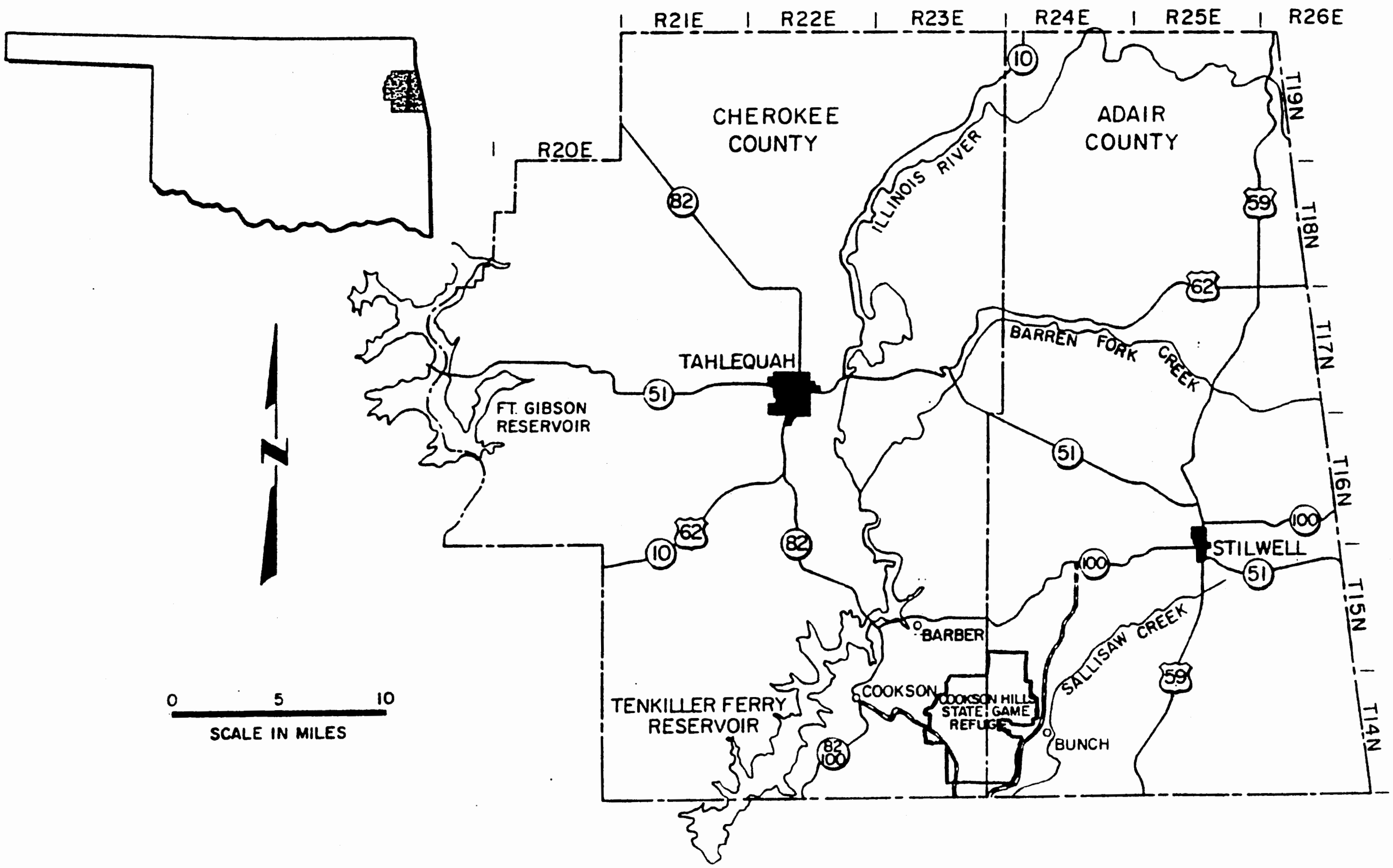

Figure 3. Map of Cherokee and Adair Counties, Oklahoma, showing location of the Cookson Hills Wildlife Management Area (From Savage 1976).

range, shortleaf pine (P. echinata)-oak, red oak (Q. rubra)-white oak (Q. alba)-hickory, bitternut hickory (C. cordiformis)-black oak-elm (Ulmus spp.) and black oak-maple (Acer spp.). Savage (1976) also identified meadows and old fields as major habitat types on Cookson (Fig. 4). These open areas are approximately 206 ha and are managed as food plots, of which 85 ha are planted with a mixture of orchard grass (Dactylis glomerata) and ludino clover (Trifolium sp.) and cut with a sickle bar and baled once every summer to reduce thatch build-up and encourage new growth. The remaining 121 ha managed as food plots are cut annually with a rotary brush mower or are left to grow with only periodic brush removal (J. Fletcher, Okla. Dep. Wildl. Conserv., pers. commun.). A complete discussion of soils, plant species, vegetative communities and habitat types can be found in Savage (1976).

Climate at Cookson is continental with dry mild winters and hot, dry, long summers with high relative humidity. Winds are generally from the south and evaporation is higher than precipitation. A complete description of the climate for Cherokee and Adair counties can be found in Cole (1970), and a summary is contained in Savage (1976).

Cookson is located in the Cookson Hills, which are an extension of the Boston Mountains extending from western Arkansas into eastern Oklahoma. The entire area is part of the Ozark physiographic region (Savage 1976). Cookson is dominated by 2 flat-topped, north-south running ridges (the

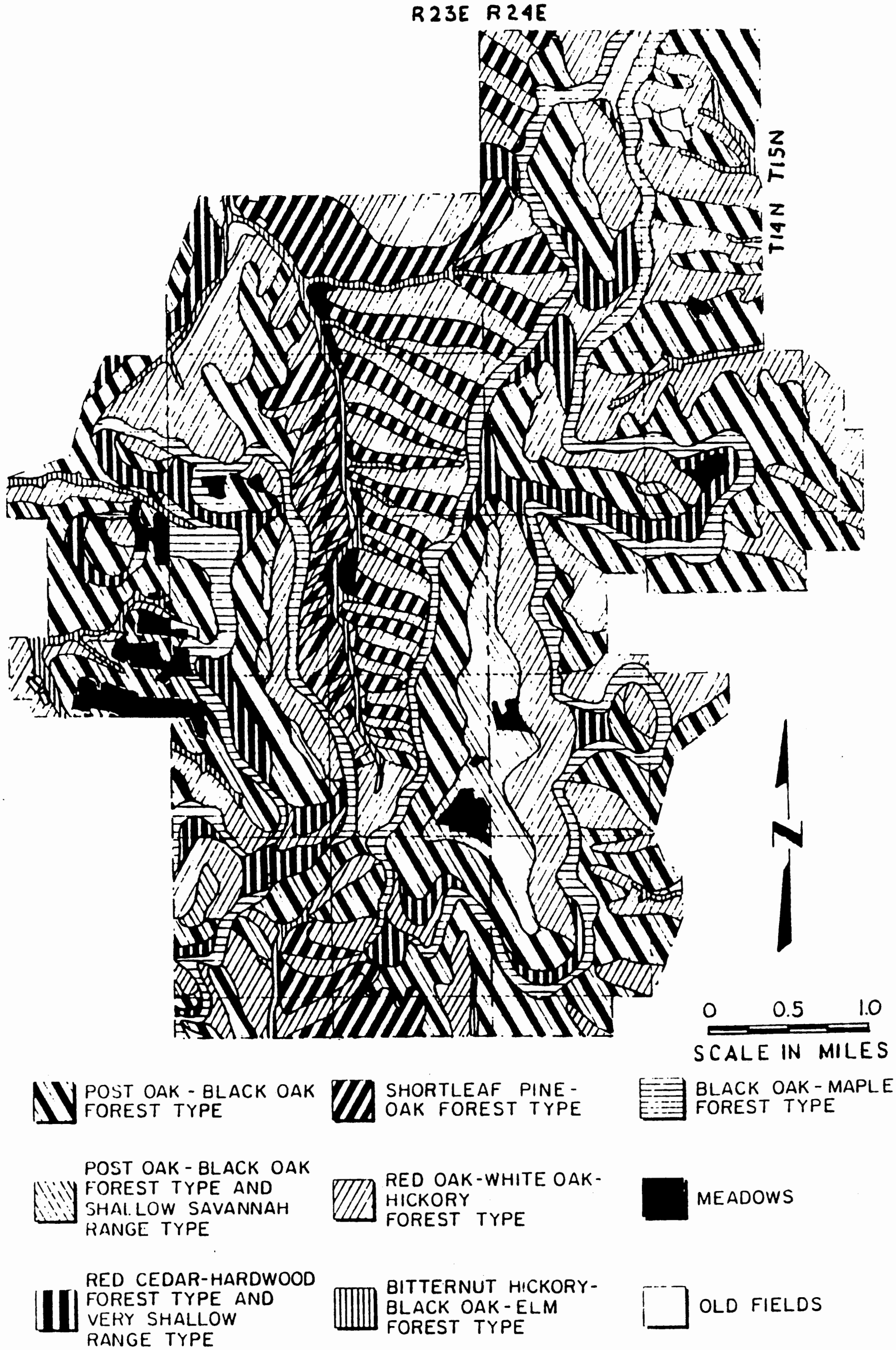

Figure 4. Map of Cookson Hills Wildlife Management Area showing distribution of major habitat types (From Savage 1976).

un-named ridge east of Bolin Hollow and Beaver Mountain) with smaller ridges running east-west off of the main ridges (Fig. 5). The highest point on Cookson is 472 m (above mean sea level) on Beaver Mountain and the lowest points (229 m) are in Walking Stick Hollow and in Bolin Hollow. Slopes range from <3% to >50% (Savage 1976). Steep slopes, loose cherts, and several creeks make vehicular travel difficult.

My research was conducted west of Beaver Mountain (Fig. 5). That area contained the majority of the food plots on Cookson and was more easily accessible by vehicle than the area located east of Beaver Mountain.

The white-tailed deer population on Cookson was estimated to be 966 in 1957, and it reached a peak in 1970 with an estimated 4,233 deer (1 deer/1.3 ha). The deer populations during my study in 1985 and 1986 were estimated at 710 and 711, respectively (Okla. Dep. Wildl. Conserv. 1989). Large numbers of deer are harvested annually on a controlled permit basis.

During January-March 1969 and February 1970, 55 non-migratory Rocky Mountain elk were trapped on the Wichita Mountains National Wildlife Refuge and moved to Cookson. Thirty-three cows and 22 bulls were re-introduced (J. Fletcher, pers. commun.); at least 3 cows and 3 bulls were young and the rest were adults (Fletcher 1969, 1970). From 1969 to 1970 at least 4 elk were shot illegally on Cookson, 1 cow was killed by a car, and one cow died of unknown causes (J. Fletcher, pers. commun.). Fletcher (pers.

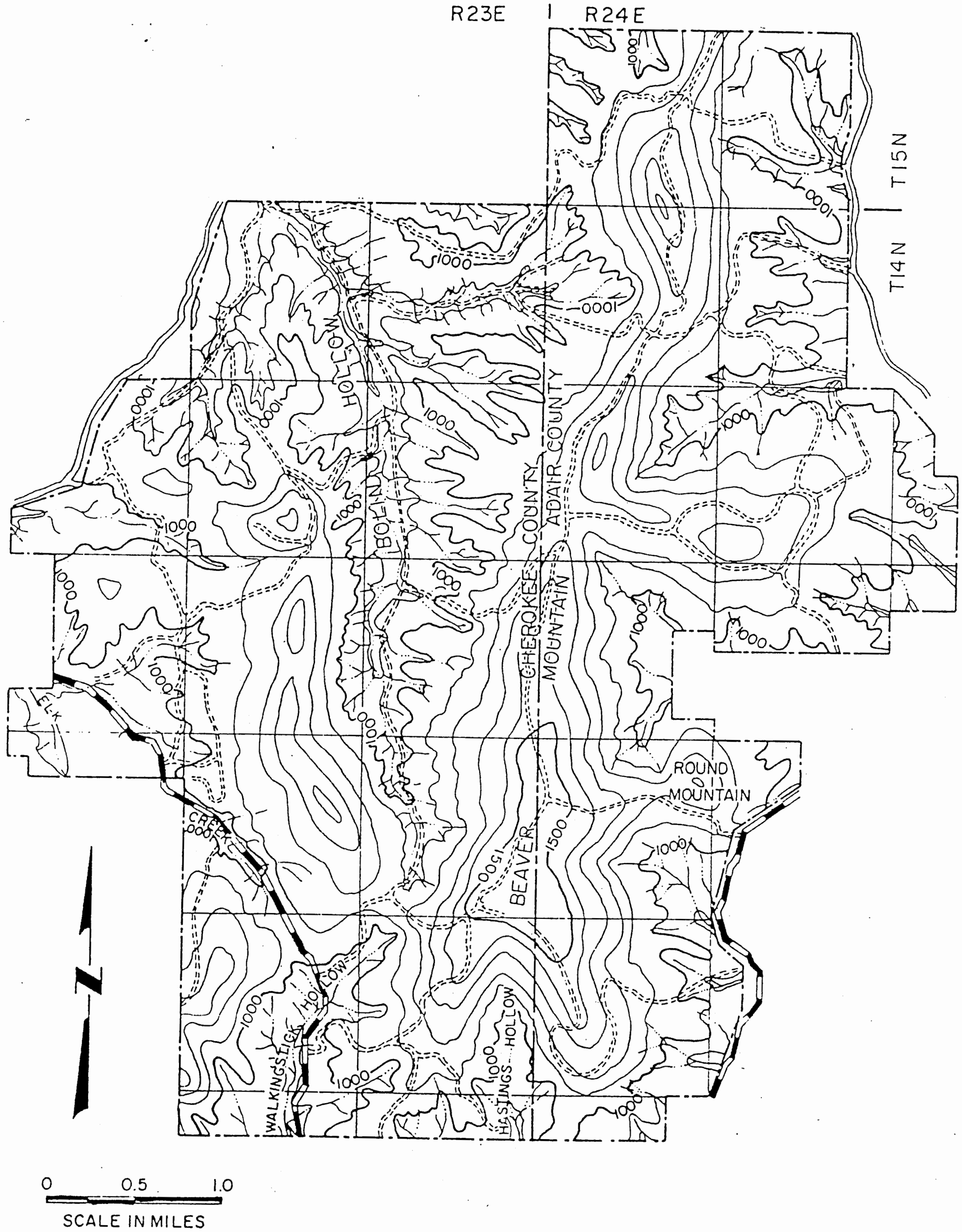

Figure 5. Topographic map of the Cookson Hills Wildlife Management Area (From Savage 1976).

commun.) indicated many of the elk just disappeared after release and some were seen "miles" from Cookson. The population of elk grew to approximately 150 and has been relatively stable even with a limited hunt.

The rugged and somewhat remote location of Cookson limits its use by non-hunters. During special hunts held on the area there is a great deal of human disturbance of the deer and elk. During winter, spring, summer, and early fall, human disturbance is minimal. Oklahoma Department of Wildlife Conservation personnel keep all of Cookson's gates locked at all times. Other than activities of Cookson personnel, the only disturbance to deer and elk are researchers on the area, occasional wood cutting, horseback riders, hikers, and mowing of the food plots in late summer. Vehicle access is limited and year-round recreational use of Cookson is not encouraged, to limit disturbance of deer and elk. However, recreation on foot or on horseback is allowed.

The primary management objective of the Oklahoma Department of Wildlife Conservation on Cookson is to create habitat conditions conducive to all wildlife species. Secondarily, the Oklahoma Department of Wildlife Conservation is trying to increase carrying capacity of Cookson for white-tailed deer by increasing habitat diversity and maintaining areas of early successional stages and forest openings. This will allow liberal harvests and increased opportunities for Oklahoma sportsmen (Okla. Dep. Wildl. Conserv. 1982).

CHAPTER III

METHODS

My research was conducted from June through August 1985 and from March through June 1986, which coincided with presumed activity periods of terrestrial gastropods. Habitat use by deer and elk was evaluated using mobile observation techniques and pellet group surveys.

Mobile Observation Techniques

Many of the food plots on the study area were accessible by gravel road or were within walking distance of a road. An observation route was established that ran from Cookson's Headquarters in a northerly direction to encompass Bolin Hollow and passed out through the north gate of the management area (Fig. 6). This route also could be travelled in the opposite direction. In 1985 and 1986, this route, or portions thereof, was generally driven in early morning or late evening hours, but late morning and afternoon observations also were included. In 1986, 20 nights of spotlight observations were made in addition to daytime observations. Observations were made in all weather conditions as they occurred.

Twenty-three food plots were included routinely in the

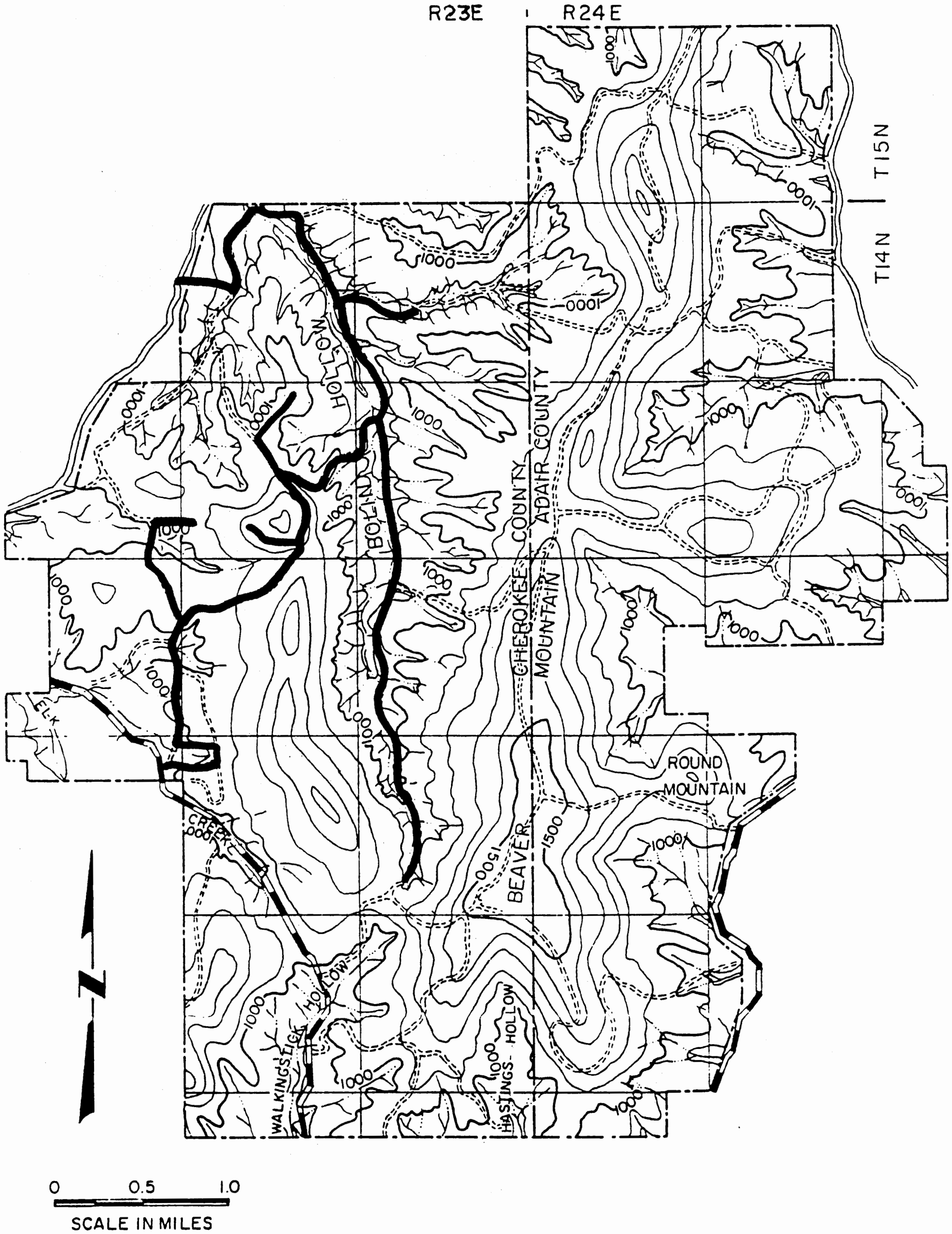

Figure 6. Map of the Cookson Hills Wildlife Management Area showing mobile observation route used to census white-tailed deer and elk in 1985 and 1986.

observations; several food plots along the mobile route were excluded because they could not be reached by a 2-wheel drive truck and were not within a reasonable walking distance of roads. Complete randomization of the order in which food plots and other habitat types were observed was not possible, but direction of travel on the mobile route was randomized. Use of a consistent mobile route was found to be advantageous with respect to food plots and habitat types surveyed per unit time (Fig. 6).

Circular Plot and Rectangular Pellet Transect Techniques

Pellet group surveys were conducted using 204 permanent 0.004-ha circular plots and permanent 2-m wide rectangular transects. Thirteen transects were established on east-west compass bearings within the study area. Eight transects were located in Bolin Hollow and 5 were along the road leading north into Cookson from the headquarters. Placement of pellet transects and plots in these areas allowed habitat use data to be collected using observations and pellet groups on the same forested areas, food plots, and general habitat types. Transects ranged in length from 610 to 1463 m and, because of the largely north-south drainage patterns on the area, each transect encompassed near maximum elevational change. The transects were marked with blue flagging so that the exact location of each transect was known and transects could easily be relocated. At 61-m intervals along each transect, 60-cm blue metal stakes were driven into the ground to an above ground height of 16 cm. These stakes were used to delineate the exact center of the permanent circular pellet plots located along the transects. Blue stakes and flagging were used to counter the possible effect that orange or other bright colors might have upon a hunted deer population.

A pellet group was defined as ≥ 5 pellets in close proximity and having similiar size, shape, and texture. A pellet group was counted as in the plot or on the transect if the lineal midpoint of the group or 50% of the area covered by the group was within the plot boundary (Neff 1968, Freddy and Bowdan 1983). Circular plot boundaries were determined by extending a 3.59-m rope from the stake in the center of the plot. Smith (1968) indicated that where pellet densities were low, 0.004-ha plots were faster to survey per unit time than smaller plots and that fewer plots were needed to gain equal precision. A meter stick was used to determine if a pellet group was within the 2-m wide transect.

Both plots and transects were initially cleared in 1985 and 1986 to eliminate difficulties associated with lost or decayed pellet groups and aging pellet groups. In 1985, all plots and transects were examined 4 times after the initial clearing and in 1986 all plots, and transects were examined 4 times and half were examined 5 times. Circular plots and transects did not overlap so that data could be collected separately. Throughout the study, all elk and deer pellet groups were collected, bagged, labeled, and frozen. Fecal samples were analyzed for P. tenuis larvae using the Baermann technique (Kocan 1985).

Gastropod Techniques

Gastropods were collected by random searching under rocks, logs, leaf litter, etc. primarily along pellet transects but also occasionally in other areas.

Lankester and Anderson (1968) found that using moistened corrugated cardboard to attract terrestrial gastropods was efficient and allowed for quantitative determination of abundance. Cardboard sheets could not be kept moist enough to provide suitable snail habitat in the hot, dry conditions present on Cookson, even when they were later covered with plastic sheeting to decrease evaporation. W. M. Samuel (Dep. Zool., Univ. of Alberta, Can., pers. commun.) indicated that he also was unable to use this technique with much success. He suggested collecting 0.05 square meter x 5 cm soil and litter samples, placing them individually in plastic containers (shoe boxes, small buckets, etc.), and wetting them for 2 days until the litter was almost submerged and retreating gastropods could be collected. This technique also failed.

After gastropods were collected, they were wrapped in moist paper towels and refrigerated for storage. Gastropods were later digested in a solution made with 6 g of pepsin, 7 ml concentrated hydrochloric acid and 1000 ml distilled water, and P. tenuis larvae were counted (Kocan 1985).

To verify that larvae found in deer feces were P. tenuis and to determine which gastropod species might be able to sustain P. tenuis infection, 4 species of snail were artificially infected using the procedure outlined by Kocan (1985). These snails were later digested and larvae from 3 species were used to infect 3 captive deer kept at Camp Redlands (Stillwater, Okla.).

Habitat Type Identification

I used habitat types identified, described, and mapped by Savage (1976) (Fig. 4); however, "edge" habitat types were added as a group because of the importance of edge ecologically. Many of the transitional areas between forest types were not readily identifiable but edge between food plots and forest types was easily identified.

Two methods were used to determine habitat availabilities in the study area. The first method entailed identifying the habitat type for each of the 204 circular pellet plots and using this information to determine habitat percentages for statistical analysis of circular pellet plot data. The second method used to determine habitat percentages for rectangular pellet transect and observational data was to walk transects and measure distances along transects that were in each habitat type. Maps and descriptions from Savage (1976) were used to identify specific habitat types (Table 2).

Statistical Analysis

Statistical analysis of pellet group and mobile observation data followed the procedure outlined by Neu et al. (1974) and clarified by Byers et al. (1984). A chi-square goodness of fit test ($P < 0.05$) was used to determine if there was a significant difference between expected pellet group frequency in each habitat type based on their availabilities and observed pellet group frequency. A chi-square goodness of fit test also was used to determine if there was a significant difference between expected use of all habitat types and observed use of habitat types based on observational data. When significant differences were found, Bonferroni z confidence intervals were constructed to evaluate pellet group frequencies and habitat usage and preference based upon observations of deer and elk.

Habitat types with no pellet groups or no observations were not included in the chi-square and were assumed to be avoided.

For the Bonferroni z-statistic to be used all observations must be independent (Alldredge and Ratti 1986). For animals that tend to herd or group including white-tailed deer and elk this assumption may not be valid. Nevertheless, all animals used in this study did have the ability to move independently. Fawns and calves were not included in the analysis because they were not independent

TABLE 2. Habitat type abbreviations and descriptions used in this study (Based upon Savage 1976).

Abbreviation	Habitat Description
Post oak	Post oak - black oak forest type
Savannah	Post oak - black oak forest type and shallow savannah range type (not found east of Beaver Mountain in study area)
Red cedar	Red cedar - Hardwood forest type and very shallow range type
Pine	Shortleaf pine - oak forest type
Red oak	Red oak - white oak - hickory forest type
Hickory	Bitternut hickory - black oak - elm forest type
Black oak	Black oak - maple forest type
Meadow	Meadows (food plots)
Field	Old fields (food plots)
Edge	Edges between food plots and forest

of does and cows. It also was assumed that habitat availability was the same for all animals. Alldredge and Ratti (1986) indicated that for this method to be used the number of habitats should be small and the numbers of animals and observations large, criteria which my data also meet. Alldredge and Ratti (1986) stated that this method of statistical analysis may be used for flushes from systematic transects, survey of random plots, or radio telemetry. The observational and pellet group data in my study approximate those types of data collection.

In my study simultaneous confidence intervals constructed around observational data were assumed to accurately reflect habitat use and preference by deer and elk because observations of deer and elk are actual samples of habitat use. Simultaneous confidence intervals constructed around pellet group frequencies were assumed to only reflect habitat differences in pellet group frequencies and do not necessarily reflect actual habitat use.

CHAPTER IV

RESULTS

Pellet Group Transect Results

During my study 154 deer pellet groups and 491 elk pellet groups were found on pellet transects. When food plots (meadows, and old fields) were combined and forest and edge habitat types were combined, no significant differences were seen between observed and expected distribution of deer pellet groups. Deer pellet groups were distributed equally throughout forests and food plots in proportion to the habitats' availability. Elk pellet groups, however appeared on food plots more frequently than they did on forested habitat types in relation to each habitats' availability (Table 3).

When habitat types were not combined but were analyzed and evaluated individually, deer pellet groups were found on meadows more than meadows were available and on old fields and red cedar-hardwood forest type and very shallow range type less than those habitats were available. On all other habitat types including edge, deer pellet groups were found in proportion to the habitats' availability (Table 4).

Elk pellet groups were found on meadows more than

Table 3. Distribution of deer and elk pellet groups between food plot and forested habitat types from pellet transects, spring and summer combined.

		Species			
		Deer		Elk	
Habitat	% Avail.	Pellet Groups	Habitat Selectivity[a]	Pellet Groups	Habitat Selectivity[a]
Food Plots	27.1	51	0	445	+
Forest	72.9	103	0	46	-

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = more than expected, 0 = equal with expected, - = less than expected ($P < 0.05$).

TABLE 4. Distribution of deer and elk pellet groups from pellet transect data, spring and summer combined.

		Species			
		Deer		Elk	
Habitat	% Avail.	Pellet Groups	Habitat Selectivity[a]	Pellet Groups	Habitat Selectivity[a]
Post oak[b]	12.8	20	0	11	–
Red cedar	2.9	1	–	0	–
Pine	7.5	9	0	0	–
Red oak	25.9	38	0	17	–
Hickory	8.4	14	0	3	–
Black oak	6.9	7	0	3	–
Meadow	21.3	50	+	422	+
Field	4.0	1	–	19	0
Edge	10.3	14	0	16	–

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = more than expected, 0 = equal with expected, – = less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

meadows were available; only 104.4 pellet groups were expected and 422 were found. Elk pellet groups were found on old fields in proportion to availability and on all other habitat types including edge, elk pellet groups were found less than the habitats' availability (Table 4).

Pellet Group Circular Plot Results

During my study 42 deer pellet groups and 174 elk pellet groups were found on circular plots. This sample size was approximately 33% of the pellet transect sample size. Although results for circular pellet plots and pellet transects did not show exactly the same patterns, the results generally agreed. When all forested and edge types were combined and food plots (meadows, and old fields) were combined, deer pellet groups occurred on forest and food plots in proportion to availability. Elk pellet groups however, occurred on food plots more than expected and forested plots less than expected (Table 5). When habitats were analyzed individually there were no differences between deer pellet group distribution and the availability of each habitat (Table 6).

Like pellet transects, circular pellet plots showed that elk pellet groups were found on meadows more than expected. Elk pellet groups were found on old fields and edge in proportion to their availability and on all forest habitat types less than they were available (Table 6).

Table 5. Distribution of deer and elk pellet groups between food plot and forested habitat types from circular pellet plots, spring and summer combined.

		Species			
		Deer		Elk	
Habitat	% Avail.	Pellet Groups	Habitat Selectivity[a]	Pellet Groups	Habitat Selectivity[a]
Food Plots	26	10	0	154	+
Forest	74	32	0	20	-

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = more than expected, 0 = equal with expected, - = less than expected ($P < 0.05$).

Table 6. Distribution of deer and elk pellet groups from circular pellet plots, spring and summer combined.

		Species			
		Deer		Elk	
Habitat	% Avail.	Pellet Groups	Habitat Selectivity[a]	Pellet Groups	Habitat Selectivity[a]
Post oak[b]	12.3	2	0	1	-
Red cedar	2.9	1	0	1	-
Pine	7.4	2	0	0	-
Red oak	25.5	9	0	5	-
Hickory	10.3	6	0	6	-
Black oak	6.9	2	0	0	-
Meadow	20.1	10	0	132	+
Field	3.9	0	0	14	0
Edge	10.8	10	0	15	0

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = more than expected, 0 = equal with expected, - = less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

Observations of Elk

During my study 3,892 elk observations (not including calves) were tallied. During spring and summer combined, adult and sub-adult elk used meadows over 4X as frequently as would be expected. Old fields were used in proportion to their availability, and all other habitat types including edge were used less than they were available.

When the spring and summer were split coinciding with the average period of gestation of elk (before mid-June), and average period of lactation for elk (after mid-June), the data for elk did not depart from spring and summer combined. During gestation, no elk were seen in red oak-white oak-hickory forest type. During lactation, elk seemed to increase their use of meadows. Elk still used old fields in proportion to their availability, and all other habitats less than they were available. During lactation, no elk were observed using red cedar-hardwood forest type and shallow range type, shortleaf pine-oak forest type, or black oak-maple forest type (Table 7).

Observational data of all cows (reproductive age, sub-adult and unidentified), except calves, were consistent with results for total elk observations. There were 3,163 cow observations during spring and summer. During spring and summer all age groups of cows preferred meadows and used old fields in proportion to their availability, while all other habitats were used less than they were available. During

Table 7. Elk habitat use from observational data (calves not included).

		Season					
		Spring		Summer		Combined	
Habitat	% Avail.	Obs.	Habitat Selectivity[a]	Obs.	Habitat Selectivity[a]	Obs.	Habitat Selectivity[a]
Post oak[b]	12.8	5	-	8	-	13	-
Red cedar	2.9	7	-	0	-	7	-
Pine	7.5	2	-	0	-	2	-
Red oak	25.9	0	-	2	-	2	-
Hickory	8.4	7	-	1	-	8	-
Black oak	6.9	32	-	0	-	32	-
Meadow	21.3	1634	+	1888	+	3522	+
Field	4.0	65	0	105	0	170	0
Edge	10.3	104	-	32	-	136	-

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = preferred, 0 = no preference, - = used less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

gestation similar results were evident, except that no cows were seen in red oak-white oak-hickory forest type. During lactation cows used meadows more frequently, and no cows were seen in red cedar-hardwood forest type and shallow range type, shortleaf pine-oak forest type, or black oak-maple forest type (Table 8).

Accurate age-class identification of cows was often difficult, but adult cows with calves could often be identified. Because of this, they are the only age-class of cows that could be analyzed separately. Adult cows of reproductive age were identified and observed 1,467 times. They used meadows preferentially and used old fields in proportion to their availability throughout the spring and summer combined. All other habitats were used less than they were available. During gestation, adult cows used habitat in the same manner as in spring and summer combined. However, during lactation, adult cows increased use of meadows (the number of observations in summer was less than spring but the percentage confidence interval derived for summer was greater than that for spring and does not overlap the spring confidence interval). Old fields were used by adult cows in proportion to their availability, and all other habitat types were used less than they were available. (Table 9).

The ease with which bulls could be separated into adult and sub-adult age-classes allowed analysis of these 2 age-classes individually. A total of 246 observations of adult

Table 8. Total cow elk habitat use from observations (calves not included).

		Season					
		Spring		Summer		Combined	
Habitat	% Avail.	Obs.	Habitat Selectivity[a]	Obs.	Habitat Selectivity[a]	Obs.	Habitat Selectivity[a]
Post oak[b]	12.8	4	-	8	-	12	-
Red cedar	2.9	7	-	0	-	7	-
Pine	7.5	1	-	0	-	1	-
Red oak	25.9	0	-	2	-	2	-
Hickory	8.4	7	-	1	-	8	-
Black oak	6.9	28	-	0	-	28	-
Meadow	21.3	1349	+	1502	+	2851	+
Field	4.0	56	0	88	0	144	0
Edge	10.3	88	-	22	-	110	-

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = preferred, 0 = no preference, - = used less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

Table 9. Adult cow elk habitat use from observations.

		Season					
		Spring		Summer		Combined	
Habitat	% Avail.	Obs.	Habitat Selectivity[a]	Obs.	Habitat Selectivity[a]	Obs.	Habitat Selectivity[a]
Post oak[b]	12.8	2	-	3	-	5	-
Red cedar	2.9	4	-	0	-	4	-
Pine	7.5	0	-	0	-	0	-
Red oak	25.9	0	-	0	-	0	-
Hickory	8.4	7	-	0	-	7	-
Black oak	6.9	19	-	0	-	19	-
Meadow	21.3	965	+	360	+	1325	+
Field	4.0	36	0	13	0	49	0
Edge	10.3	54	-	4	-	58	-

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = preferred, 0 = no preference, - = used less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

bulls was made during the study. Adult bulls used meadows preferentially and old fields in proportion to their availability. All other habitats were used less than they were available. Habitat use by adult bulls during spring and summer individually was the same as spring and summer combined (Table 10). Sub-adult bulls (not including calves) were observed 471 times during spring and summer combined. Sub-adult bulls used habitats in the same manner as did adult bulls (Table 11).

Meadows were used preferentially by both sexes and all age-classes of elk. Of 3,522 observations of elk (not including calves) in meadows, 51.8% of the elk were feeding, 26.8% were bedded, and 20.0% were standing or walking.

Observations of Deer

During my study 742 adult deer were observed. For spring and summer combined deer used food plots (meadows, and old fields) preferentially. Deer used edge and red cedar-hardwood forest type and very shallow range type in proportion to their availabilities, and all other habitat types less than they were available. Data from spring were the same as for spring and summer combined. During summer, deer used food plots preferentially, but all other habitat types were used less than they were available (Table 12).

Antlerless deer were observed 635 times during the study. For spring and summer combined, antlerless deer used food plots (meadows, and old fields) preferentially.

Table 10. Adult bull elk habitat use from observations.

Habitat	% Avail.	Spring Obs.	Spring Habitat Selectivity[a]	Summer Obs.	Summer Habitat Selectivity[a]	Combined Obs.	Combined Habitat Selectivity[a]
Post oak[b]	12.8	0	-	0	-	0	-
Red cedar	2.9	0	-	0	-	0	-
Pine	7.5	1	-	0	-	1	-
Red oak	25.9	0	-	0	-	0	-
Hickory	8.4	0	-	0	-	0	-
Black oak	6.9	0	-	0	-	0	-
Meadow	21.3	94	+	129	+	223	+
Field	4.0	5	0	5	0	10	0
Edge	10.3	5	-	7	-	12	-

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = preferred, 0 = no preference, - = used less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

Table 11. Sub-adult bull elk habitat use from observations (calves not included).

Habitat	% Avail.	Spring Obs.	Spring Habitat Selectivity[a]	Summer Obs.	Summer Habitat Selectivity[a]	Combined Obs.	Combined Habitat Selectivity[a]
Post oak[b]	12.8	1	-	0	-	1	-
Red cedar	2.9	0	-	0	-	0	-
Pine	7.5	0	-	0	-	0	-
Red oak	25.9	0	-	0	-	0	-
Hickory	8.4	0	-	0	-	0	-
Black oak	6.9	4	-	0	-	4	-
Meadow	21.3	191	+	246	+	437	+
Field	4.0	4	0	11	0	15	0
Edge	10.3	11	-	3	-	14	-

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = preferred, 0 = no preference, - = used less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

Table 12. Adult deer habitat use from observations.

		Season					
		Spring		Summer		Combined	
Habitat	% Avail.	Obs.	Habitat Selectivity[a]	Obs.	Habitat Selectivity[a]	Obs.	Habitat Selectivity[a]
Post oak[b]	12.8	11	-	14	-	25	-
Red cedar	2.9	9	0	5	-	14	0
Pine	7.5	13	-	2	-	15	-
Red oak	25.9	10	-	5	-	15	-
Hickory	8.4	8	-	15	-	23	-
Black oak	6.9	10	-	12	-	22	-
Meadow	21.3	171	+	294	+	465	+
Field	4.0	55	+	44	+	99	+
Edge	10.3	40	0	24	-	64	0

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = preferred, 0 = no preference, - = used less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

Antlerless deer used edge red cedar-hardwood forest type and very shallow range type in proportion to their availabiliies. All other habitat types were used less than expected by their availabilities. During spring, antlerless deer habitat use did not change from spring and summer combined. During summer, antlerless deer used all habitats the same as in spring except that edge was used less than it was available (Table 13).

Only 107 positive buck observations were made during my study, and 90 of these were made during summer. It is possible that bucks were misidentified as does during the early spring and were included in the antlerless deer totals, which would account for the low number of buck observations during the spring. This low number of observations rendered results from chi-square and Bonferroni confidence intervals questionable; thus, buck data were only analyzed for spring and summer combined. During spring and summer combined, bucks used food plots preferentially. Bucks used red cedar-hardwood forest type and very shallow range type and edge in proportion to their availabilities. All other habitat types were used less than expected on the basis of availability. Buck and antlerless deer data showed the same habitat use trends (Table 14).

Food plots (meadows and old fields) were preferentially used by both sexes of deer throughout spring and summer. A total of 465 adult deer was observed in meadows; 62.2% were feeding, 14.4% were standing or walking,

Table 13. Antlerless deer habitat use from observations.

Habitat	% Avail.	Spring Obs.	Spring Habitat Selectivity[a]	Summer Obs.	Summer Habitat Selectivity[a]	Combined Obs.	Combined Habitat Selectivity[a]
Post oak[b]	12.8	11	-	12	-	23	-
Red cedar	2.9	7	0	4	0	11	0
Pine	7.5	13	-	2	-	15	-
Red oak	25.9	9	-	5	-	14	-
Hickory	8.4	8	-	14	-	22	-
Black oak	6.9	10	-	12	-	22	-
Meadow	21.3	165	+	223	+	388	+
Field	4.0	50	+	33	+	83	+
Edge	10.3	37	0	20	-	57	0

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = preferred, 0 = no preference, - = used less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

Table 14. Buck deer habitat use from observations, spring and summer combined.

Habitat	% Avail.	Obs.	Habitat Selectivity[a]
Post oak[b]	12.8	2	-
Red cedar	2.9	3	0
Pine	7.5	0	-
Red oak	25.9	1	-
Hickory	8.4	1	-
Black oak	6.9	0	-
Meadow	21.3	77	+
Field	4.0	16	+
Edge	10.3	7	0

[a] Chi-square analyses followed by Bonferroni confidence intervals (Neu et al. 1974); + = preferred, 0 = no preference, - = used less than expected ($P < 0.05$).

[b] Habitat abbreviations refer to Table 2.

and 10.5% were bedded. A total of 99 observations was made in old fields; 37.4% were feeding, 24.2% were standing or walking, and 29.3% were bedded.

Gastropod Results

I found 2,513 gastropods of 15 different species. The most common species encountered was Helicina orbiculata. Sixty-five P. tenuis larvae were recovered from 959 gastropods digested (0.07 larvae/gastropod). No larvae were found in 7 species of gastropods, but Triodopsis divesta contained 0.30 larvae/snail (Table 15). If gastropods were digested individually, a percentage of infected gastropods could be determined. But, because many of the gastropods were digested in groups of 5, a percentage of infected gastropods could not be determined.

Gastropods were found most often in red cedar-hardwood forest and very shallow range type, but, they also were encountered in other forested habitats as well. Areas of red oak-white oak-hickory that were on north- and east-facing slopes on Cookson had particularly high gastropod densities. Only 4 gastropods were found in food plots (3 T. divesta and 1 Stenotrema stenotrema), and only 2 were found in the edge between food plots and forest (1 T. divesta and 1 Mesodon inflectus). Most habitat types had a very low number of P. tenuis larvae/gastropod (0-0.06 larvae/gastropod), but in red oak-white oak-hickory forests, the average number of larvae/gastropod was 0.34 (Table 16).

Table 15. Total gastropods found and *P. tenuis* larvae by gastropod species.

Species	Number Found	Number Digested	Larvae Found	Larvae/ Gastropod
Anguispira alternata	19	7	0	0
Bulimulus dealbatus	28	21	0	0
Deroceras laeve	46	13	0	0
Discus cronkhitei	9	9	0	0
Discus patulus	637	129	1	0.01
Helicina orbiculata	797	263	9	0.03
Mesomphix cupreus	10	10	1	0.10
Mesodon inflectus	52	33	8	0.13
Mesodon thyroidus	2	1	0	0
Polygyra dorfeuilliana	172	113	11	0.10
Polygyra jacksoni	303	194	7	0.04
Stenotrema stenotrema	139	70	3	0.04
Triodopsis albolabris	21	9	0	0
Triodopsis divesta	250	83	25	0.30
Zonitoides arboreus	12	4	0	0
Total	2513	959	65	0.07

Table 16. Total gastropods found and *P. tenuis* larvae by habitat type.

Habitat	Number Found	Number Digested	Larvae Found	Larvae/ Gastropod
Post oak[a]	291	181	7	0.04
Red cedar	873	292	14	0.05
Pine	24	8	0	0
Red oak	649	74	25	0.34
Hickory	311	197	11	0.06
Black oak	174	83	3	0.04
Meadow	4	1	0	0
Field	0	0	0	0
Edge	2	0	0	0
Unknown	185	123	5	0.04
Total	2513	959	65	0.07

[a] Habitat abbreviations refer to Table 2.

Gastropods were found in a variety of microhabitats including on or amidst herbaceous vegetation, on or under the leaf litter, under rocks, ledges, logs, and on a tar road. Gastropods were most commonly found on or amidst herbaceous vegetation (824) but were also often found on or under the leaf litter (647). The gastropods found in most microhabitats ranged from 0 to 0.06 larvae/gastropod. However, gastropods found under rocks and on or in the leaf litter had 0.12 and 0.22 larvae/gastropod, respectively (Table 17).

Gastropods infected artificially with _P_. _tenuis_ larvae included the snails _Bulimulus dealbatus_ (4), _Helicina orbiculata_ (30), _Mesodon cupreus_ (5), and _Triodopsis divesta_ (24). Even when exposed to large numbers of larvae _M_. _cupreus_ was only infected with 0.4 larvae/snail. _H_. _orbiculata_ and _B_. _dealbatus_ were able to maintain infections of 10.87 and 18.5 larvae/snail, respectively. _T_. _divesta_ was able to maintain an infection of 71.0 larvae/snail.

Three captive deer were artificially infected with third stage _P_. _tenuis_ larvae digested out of gastropods. One deer infected with larvae from _B_. _dealbatus_ soon died of other causes. The 2 remaining deer had no _P_. _tenuis_ larvae in their feces after 99 days, but after 122 days the deer infected with larvae from _H_. _orbiculata_ had 1 larva in 39 g of wet feces. After 157 days, 1 larva was found in 14.3 g of wet feces from the deer infected with larvae from _H_. _orbiculata_ and 4 larvae were found in 46.2 g of wet feces

Table 17. Total gastropods found and *P. tenuis* larvae by micro-habitat type.

Micro-Habitat	Number Found	Number Digested	Larvae Found	Larvae/ Gastropod
Herb. Veg.	824	284	8	0.03
Ledge	45	17	0	0
Litter	647	78	17	0.22
Log	374	125	7	0.06
Rock	332	185	22	0.12
Rocks/Logs	125	125	4	0.03
Tar Road	2	1	0	0
Unknown	164	144	7	0.05
Total	2513	959	65	0.07

from the deer infected with larvae from *T. divesta*. That same week the deer infected with larvae from *T. divesta* was inadvertently killed for another experiment. At 172 days post-infection the deer that was left, which had been infected with larvae from *H. orbiculata* was killed and necropsied. One adult *P. tenuis* was found in the brain, and no larvae were found in 13.9 g of wet feces.

Baermann Results

Both deer and elk feces were analyzed for *P. tenuis* larvae, but no clear results could be obtained. Most of the pellets were not fresh when collected and numerous other species of nematodes were found, which made identification of larvae very difficult. A sample of nematodes shown to A. A. Kocan (Dep. Vet. Med., Okla. State Univ.) from elk feces did not include any *P. tenuis* larvae; a sample of nematodes from deer feces did include *P. tenuis* larvae.

CHAPTER V

DISCUSSION

Anderson and May (1978) defined host-parasite systems as a class of predator-prey interactions and indicated that a parasite must use the host as habitat, be nutritionally dependent on the host, and cause harm to the host (increase death rate and/or decrease fecundity). Anderson and May (1978) also defined a parasite as a species that does not kill its host as part of the parasite's life cycle (if it does it is a parasitoid). *P. tenuis* satisfies these conditions for white-tailed deer and gastropods (although the 'harm' may be very slight). *P. tenuis* usually causes death in abnormal hosts such as elk. Woolf et al. (1977) found adult *P. tenuis* in elk cranial cavities, but they did not examine whether the entire life cycle of *P. tenuis* could occur in elk. Karns (1966) indicated that it was possible for elk to sustain *P. tenuis* infection long enough so that first stage larvae could be collected in feces. However, the larvae that Karns (1966) found may not have been *P. tenuis*. It is possible that elk on Cookson can harbour *P. tenuis* infection with no clinical disease symptoms. This possibility was not specifically tested in this study and no conclusions can be drawn.

It is clear from the percentage of infected white-tailed deer on Cookson and the prevalence of pellet groups on all habitat types that feces containing first stage *P. tenuis* larvae are present on all habitat types. Meadows probably contain the most larvae because they contained the most deer pellet groups. This would seem to indicate that meadows were the prime site of *P. tenuis* transmission; however, only 4 gastropods were found on meadows during the entire study.

Many of the meadows and old fields on Cookson were at one time cotton fields (J. Fletcher, pers. commun.) and had poor soils that are highly compacted and may be difficult for a gastropod to penetrate. The soil in the meadows was dry and covered with little thatch. In old fields the soil was dry, but more thatch was present. The top of the soil temperatures on the meadows and old fields during summer in full sun can become high on a daily basis (>38'C). These dry, hot conditions with compacted soil may limit gastropod survival on the meadows and old fields. Maze and Johnstone (1986) also found that horse pastures had low densities of snails and slugs as compared to forested areas. Meadows and old fields on Cookson do not appear to be important transmission sites of *P. tenuis*.

Gastropods were abundant in red cedar-hardwood forest type and very shallow range type, and red oak-white oak-hickory forest type. Red cedar-hardwood forest type and very shallow range type habitat were found on talpa soils that are thin, mineral, high in organic matter and, soft when dry. Thin layers of talpa soils were found overlaying limestone that weathers into the soil as fast as the soil erodes (Savage 1976). Even in the middle of summer, these areas were often moist and had a large amount of thatch built-up, which may have helped to retain moisture. In these red cedar areas, gastropods were common on vegetation and in thatch and litter on the ground. Soil characteristics (i.e., high limestone content and moistness) may permit high gastropod densities. Gastropods collected and digested from these areas were not particularly high in larvae/gastropod (0.05). The snail *H. orbiculata* was the most common gastropod found in the red cedar-hardwood forest type and very shallow range type, and it had 0.03 larvae/gastropod. Red cedar-hardwood forest type and very shallow range type may be an important transmission site of *P. tenuis*.

Gastropods also were abundant in red oak-white oak-hickory forest type, which was found on north to east facing slopes on Sallisaw, Linker, and Clarksville soils (Savage 1976). Most gastropods found in this habitat type were found in Bolin Hollow on north facing slopes with Clarksville soils. Clarksville soils are layered chert; they are well drained and soil moisture is low. At most times gastropods were rarely found in these areas either under logs or rocks, but after a rain gastropods were extremely abundant. Gastropods appeared to move through chert layers to the surface when moisture was available and, could retreat into chert when soil began to dry. The most common gastropod found in red oak-white oak-hickory forest type was *D. patulus*, which had only 0.01 larvae/gastropod, but *P. dorfeuilliana* (0.10 larvae/gastropod) and *T. divesta* (0.30 larvae/gastropod) were also common. Prevalence and availability of gastropods in the red oak-white oak-hickory forest type may make it an important site for transmission of *P. tenuis*.

At the outset of my study, I assumed that riparian bitternut hickory-black oak-elm forest type would be an important transmission site of *P. tenuis*. However, these areas are prone to flooding and are wet during spring or after a heavy rain. Most streams on Cookson are seasonal and dry up in summer. Flooding combined with summer drying appears to be detrimental to gastropod survival, possibly minimizing the importance of this habitat in *P. tenuis* transmission.

Gastropods with the highest numbers of larvae/gastropod were most often collected in or on the forest litter (0.22 larvae/gastropod). Although gastropods were more often collected on herbaceous vegetation (particularly in red cedar-hardwood forest type and very shallow range type habitat) only 0.03 larvae/gastropod were found, which suggests that deer or elk that forage down in the leaf litter, perhaps for mushrooms, acorns, etc. may be more likely to ingest infected gastropods.

Anderson and May (1978) indicated that the most common distribution of parasites within a host population is over dispersed, meaning that a relatively few hosts carry most of the parasite population. This appears to be the case with gastropods and P. tenuis on Cookson. Upshall et al. (1986) found in Canada that 2.5% of gastropods collected contained third stage P. tenuis larvae. Maze and Johnstone (1986) found third stage larvae in 9.0% of all gastropods collected in Pennsylvania. Upshall et al. (1986) and Maze and Johnstone (1986) did not indicate the number of larvae/gastropod found. Unfortunately, larvae/gastropod for individual gastropods and percentages of infected gastropods could not be determined with the methods used at Cookson, but it appeared that the low average number of larvae/gastropod (0-0.30 larvae/gastropod) could be explained by the fact that few gastropods were actually infected.

It has been assumed that deer and other ungulates ingest gastropods accidentally while foraging and that the large amount of vegetation consumed daily resulted in ingestion of many gastropods, a few of which may contain P. tenuis larvae. Gastropods are often difficult to find on Cookson and many are large (e.g.,T. divesta may reach 20 mm in diameter and T. albolabris may reach 28 mm) (Leonard 1959). It seems possible that ungulates may not ingest gastropods accidentally but may choose to eat gastropods for some unknown reason.

Both deer and elk on Cookson use meadows more than expected. It could be argued that methods used in my study over-estimated use of meadows and old fields because deer and elk may be more visible in those habitats. But, generally pellet group data showed the same trends as observations. The high quality of available forage on meadows makes them particularly attractive for feeding. Nelson and Leege (1982) indicated that grass is the most important forage for elk during spring green-up. But, as grass cures in summer it becomes less important. Cured grass and new green grass becomes more important in fall and winter when it is available. Mowing of meadows on Cookson in mid-summer maintains green grass and does not allow it to mature and cure.

Meadows were important feeding areas for both deer and elk on Cookson but are used much more frequently by elk. Elk were observed on food plots 3,522 times while deer were seen only 465 times, while the total population of deer on Cookson is estimated to be approximately 4.5X the estimated size of the elk population. It is clear that meadows are very important resources for elk. Elk may not avoid other habitats, but they used meadows in preference to other habitats. Deer seemed to use meadows and old fields most during dusk to dawn, but elk were observed in meadows during all parts of the day. From watching identifiable elk it appeared that elk move from meadow to meadow using the forest as mainly travel lanes.

While deer do use meadows and old fields they also spend more time than elk in forested habitat types. The high prevalence of P. tenuis infection among deer on Cookson and the lack of intermediate gastropod hosts on meadows and old fields indicated that deer must be feeding in habitats other than meadows and old fields. Verme and Ullrey (1984) indicate that while deer are purported to be browsers they consume a variety of foods, including grasses, sedges, fruits, nuts, forbs, mushrooms and portions of shrubs and trees. Generalist feeding habits of deer on Cookson may increase their chances of becoming infected with P. tenuis.

The special conditions on Cookson that allow the elk herd to survive may include weather patterns and management considerations such as the maintenance of food plots (meadows and old fields) and lack of public access. The sedentary behavior of the particular herd of elk found on Cookson also may be a factor. It appears that elk that do not venture into forested habitats to feed, but feed on the food plots, do not become infected with P. tenuis. When management plans are made for Cookson, 2 considerations should be taken into account; how will the plan affect deer and elk feeding patterns and how will the plan affect gastropod distribution. Management decisions to alter forest habitat types or modify the structure of food plots, either by changing forage species composition, planting and harvesting regime, or by decreasing the size of food plots to provide more cover for deer may adversely affect elk on Cookson. To insure the survival of elk on Cookson, management should be modified only after all factors have been considered and a systematic monitoring program for elk has been developed. Any management should include systematic monitoring of population numbers, age structure, habitat use and yearly necropsy of hunter killed animals to determine reproductive status, health and if *P. tenuis* are present.

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