

Michael Matheson Anderson. A HELMINTHOLOGICAL SURVEY OF SMALL WOODLAND MAMMALS FROM EASTERN NORTH CAROLINA. (Under the direction of Dr. James S. McDaniel) Department of Biology, June 1976.

Small mammals were collected in several forest communities of the coastal plain of North Carolina from December, 1973, through April, 1975. Over 12,000 trap nights yielded four species of small mammals. In order of abundance, these were the wood mouse, Peromyscus leucopus; the short-tailed shrew, Blarina brevicauda; the rice rat, Oryzomys palustris; and the house mouse, Mus musculus.

The low population density of small mammals, manifested by the poor catch, was attributed to periodic flooding, uniform pine dominance, and cultivation of many drier coastal plain sites. All of these factors reduce the amount of suitable habitat.

The four hosts harbored 17 species of helminths representing three phyla and four classes. Seven of the helminths are new state records. Boreostrongylus peromysci is reported from the wood mouse for the first time.

The short-tailed shrew exhibited an endoparasitic population larger and more varied than that of the other small mammals. This is probably correlated with the insectivorous habits and terrestrial mode of life of Blarina.

The occurrence of Capillaria americana, the most prevalent helminth infecting the wood mouse, was significantly influenced by the age of the host and the season of the year. No such effect was observed for Boreostrongylus peromysci, the second most abundant helminth occurring in P. leucopus. Neither of these endoparasites showed an important difference in the frequency or degree of infection of male or female hosts.

Pregnancy was found to significantly influence the prevalence of the total endoparasite population of P. leucopus.

Several abiotic and biotic factors are cited as influencing the distribution of helminth infections in wood mice.

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A HELMINTHOLOGICAL SURVEY  
OF SMALL WOODLAND MAMMALS FROM EASTERN NORTH CAROLINA

A Thesis  
Presented to  
the Faculty of the Department of Biology  
East Carolina University

In Partial Fulfillment  
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by  
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Dedicated to My Wife, Lenora W. Anderson

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## INTRODUCTION

"Small mammal" is a term which is generally intended to include the free-living small rodents and insectivores (Delany, 1974). The upper size limit is difficult to define and is usually set arbitrarily. Following the definition given by Golley et al. (1965), the upper size limit in the present study includes those animals that may reasonably be expected to be captured with commercial break-back mouse traps or the smallest Sherman and Havahart live traps. These animals generally weigh less than 75 grams.

Rodents and insectivores that commonly occur in forests throughout much of the eastern United States have been the subject of a considerable amount of investigation over the last few decades. However, comparatively little information is available on the small mammals occurring in southern forests. Less is known about the helminths parasitizing these woodland inhabitants. Although there have been scattered reports of internal parasites infecting the various small mammal species normally occurring in wooded areas, none of these have been from the coastal plain of North Carolina.

These small animals constitute a major part of the food supply of predatory birds, reptiles, and mammals (Blair, 1953). Consequently, they are an important component of the food chain of forest ecosystems and play a significant role

in the maintenance of stability within the forest community. Any influence that the endoparasites exert on these small mammals may affect this stability to some degree.

Coggins and McDaniel (1975) conducted an extensive survey of the helminths of the cotton rat (Sigmodon hispidus), probably the most common small mammal occurring in old field situations of the coastal plain. With the exception of their study, such information concerning the small mammals of this region is generally absent. My investigation was initiated to determine the major components of the small mammal fauna occurring in woodland habitats of coastal North Carolina and the endoparasites which commonly infect these animals. The relationship between the ecology of each animal and its internal parasites will be considered where justified by the capture of sufficient numbers of hosts.

During two years of intensive trapping in wooded areas of the coastal plain of North Carolina, the following species of small mammals were captured: the wood mouse, Peromyscus leucopus (Rafinesque); the short-tailed shrew, Blarina brevicauda Say; the rice rat, Oryzomys palustris (Harlan); and the house mouse, Mus musculus (Linnaeus). Although other species may occur in forests of this region, the wood mouse and the short-tailed shrew are undoubtedly the most abundant.

Peromyscus leucopus, which has a wide geographical

distribution in North America, has been included in several reports on helminths of rodents (Doran, 1954a, 1954b, 1955a, 1955b). Harkema (1936) included the wood mouse in his survey of the parasite fauna of five North Carolina rodents. Although important, this investigation was limited to one county in central (piedmont) North Carolina, and the majority of the wood mice were collected from one site (Duke Forest). Hall et al. (1955) included P. leucopus among several species of Maryland and Kentucky rodents investigated for endoparasites. It was the most numerous of nine species of Maryland rodents examined for intestinal nematodes (Lichtenfels and Haley, 1968). Zenchak and Hall (1971) published a list of the helminths from P. leucopus and the deer mouse, Peromyscus maniculatus, in West Virginia. The wood mouse was one of three Tennessee rodents examined by Childs and Cosgrove (1966) for internal parasites.

Comprehensive studies of the endoparasite population of B. brevicauda have been published sporadically. Boyd and Dunning (1960) published a list of the metazoan parasites of 23 short-tailed shrews collected in western Massachusetts. In Ohio, Oswald (1958) studied the helminth parasites of 93 short-tailed shrews. Most recently, Miller et al. (1974) surveyed 46 B. brevicauda from piedmont North Carolina for endoparasites.

Although there have been scattered reports of single



species of endoparasites from O. palustris, none of them concerned North Carolina. The only comprehensive study of the helminths of the rice rat was conducted by Childs and Cosgrove (1966) in Tennessee.

The cosmopolitan rodent Mus musculus has been studied extensively. The helminths infecting the house mouse have been reported from numerous localities throughout the world. In North Carolina, Harkema (1936) conducted an investigation of the parasites of house mice trapped in human dwellings.

The wood mouse was the only small mammal taken frequently enough to allow examination of some of the factors influencing the dynamics of the endoparasite fauna, such as season of the year and the sex and age of the host. However, the internal parasites recovered from all the species of small mammals trapped during the investigation will be enumerated and discussed in terms of their relationship to the host.

#### MAMMALIAN HOSTS

##### Peromyscus leucopus Wood Mouse

Brimley (1944-1946), in a series of Carolina Tips, reported that this species was probably the most common small mammal in North Carolina. It has an extensive range in Mexico and the eastern half of the United States.

The wood mouse is primarily an inhabitant of wooded

areas but has been reported to range occasionally into fields (Blair, 1948; Brown, 1964; Burt, 1940; Fleming, 1970; Getz, 1961b; Golley, 1962, 1966; Whittaker, 1967). However, extensive weedy fields not bordered by trees or shrubs are unsuitable for this species (Barbour and Davis, 1974).

The size of wood mouse populations varies from year to year (Blair, op. cit.; Golley, 1962) and seasonally (Fleming, op. cit.). Although breeding occurs throughout the year in the South, it decreases during the summer months (Asdell, 1964; Golley, 1962, 1966). As a result, lowest population densities occur in the late summer and early fall (Stickel and Warbach, 1960). McCarley (1954) stated that wood mouse populations and all other Peromyscus populations in the southeastern United States gradually increase in size beginning in September or October and continuing until February or March. Afterwards, there is a gradual decline in population size until breeding is resumed in the early fall. Populations are greatly influenced by local environmental conditions, which may occasionally completely reverse these general trends (McCarley, op. cit.).

The mean litter size of P. leucopus is four (Asdell, op. cit.). According to Rood (1966), the number of litters averages eight per year in captive females. Home ranges average between 0.04 and 1.21 hectares, and males often range further than females (Fleming, op. cit.).

Three developmental stages, juvenile, subadult, and

adult, can be identified through pelage change in P. leucopus. The post-juvenile molt begins in mice between 40 and 50 days old and lasts for 12 to 29 days (Gottschang, 1956). The age at which the post-subadult molt occurs has not been determined. In those species of the genus Peromyscus for which data are available, the post-subadult molt begins at an average age of about 15 weeks (Layne, 1968). The juvenile pelage is a bluish gray, whereas the subadult pelage is more brownish. Although the subadult pelage resembles the adult pelage, there is typically more orange-yellow in the latter.

Peromyscus leucopus exhibits considerable arboreal behavior (Burt, 1940; Getz and Ginsberg, 1968; Horner, 1954). Burt (op. cit.) has frequently caught wood mice in traps attached to tree trunks at about 1.5 meters above the ground. No significant arboreal activity has been reported for the other species of small mammals captured during the present investigation.

The rate of mortality among both juvenile and adult wood mice is very high. Blair (1948), Hirth (1958), and Stickel and Warbach (1960) estimated the average life span of P. leucopus that lived until they left the nest was less than six months.

Blarina brevicauda Short-tailed Shrew

This small slate-colored mammal occurs throughout the eastern half of the United States and Canada. It prefers moist woods, although it may occur in a variety of land habitats (Barbour and Davis, 1974; Blair, 1940; Burt, 1940; Getz, 1961a; Golley, 1962, 1966; Krull and Bryant, 1972). The home range is restricted to about 0.4 hectares (Hamilton, 1931) and tends to be larger for males (Blair, op. cit.). Only a small percentage of short-tailed shrews survive from one summer to the next in the wild (Pearson, 1945), their maximum age probably being about 20 months (Dapson, 1968). Females may have several litters per year of one to eight young (Golley, 1962). Unlike the wood mouse, which is nocturnal, B. brevicauda is active during the day and night (Barbour and Davis, op. cit.).

Oryzomys palustris Rice Rat

The rice rat has been recorded from localities throughout the southeastern United States (Hall and Kelson, 1959). In North Carolina, Brimley (1944-1946) reported records from only three counties (two coastal and one piedmont). This is the first report of O. palustris from Pitt County.

The rice rat is semiaquatic and may be relatively abundant in salt and freshwater marshes (Golley, 1962).

However, it may occur in dry fields at an elevation of more than one thousand feet (Hamilton, 1946). Although the food habits of rice rats are variable (Negus et al., 1961), the rice rat seems to prefer animal material (Sharp, 1967). Reproduction is possible throughout the year (Golley, 1966). Brimley (1923) reported pregnant rice rats in March, April, June, July, August, September, and November at Raleigh, North Carolina. Litters consisted of three to seven young (five average).

Mus musculus House Mouse

This cosmopolitan species is a common associate of man, occupying buildings of all sorts. Brimley (1944-1946) reported that the house mouse occurred as a truly feral mammal in North Carolina. I have found it to be an insignificant part of the mammalian fauna occupying woodland areas of the coastal plain of North Carolina.

## MATERIALS AND METHODS

Animals were collected with standard break-back mouse traps or Sherman and Havahart live traps (5 x 6.5 x 16.5 cm, 7.5 x 9 x 23 cm, 7 x 8 x 25.5 cm). Traps were baited with peanut butter or a mixture of peanut butter and oatmeal. Canned dog food and a peanut butter and cornmeal mixture were utilized occasionally to check the attractiveness of the bait. These baits were chosen because they are inexpensive, easy to use, and are employed by many other investigators involved in trapping small mammals. More complicated baits have not been shown to be superior to peanut butter (Jackson, 1952).

Traps were set in wooded areas in the late afternoon and checked early the next morning. The number of traps set each day varied between 30 and 100, depending largely upon the amount of favorable habitat. The traps were placed in a straight line 15 to 30 feet apart. Traplines were maintained in a locality from two to seven consecutive nights. On several occasions, traps left during the day were disturbed, stolen, or destroyed. When this occurred, I removed the traps at dawn and returned to reset them just before nightfall.

Seventeen wooded areas throughout Pitt County were trapped (Fig. 1). Small mammals were collected from 11 of these areas (2, 5, 6, 7, 9, 10, 11, 13, 15, 16, and 17). The

majority of the hosts were taken from seven locations (2,5, 6,11,13,15, and 16).

Several major upland forest communities, essentially equivalent to those described by Wells (1928), were represented among the 17 woodland localities trapped. These ranged from meso-xeric pine forests to mesophytic broadleaved forests and climatic-climax communities.

Small mammals obtained during the night were taken to the laboratory to be examined for helminths. Animals collected in live traps were killed with chloroform. If an animal could not be examined immediately, it was frozen for later study. The date, locality, sex, reproductive condition, and certain standard measurements used to determine species were recorded before autopsy (Appendix A). In addition, the pelage phase (juvenile, subadult, or adult) of each wood mouse was recorded. This, together with a knowledge of the approximate time in development when post-juvenile and post-subadult molts occur, allowed determination of the relative age. The other species of mammals could not be aged in this manner.

The heart, body cavity, bladder, viscera, alimentary canal, and associated ducts were examined both macroscopically and with a dissecting microscope. A tissue press of the diaphragm was examined for larvae of Trichinella spiralis.

Helminths were removed from the host and washed in tap

water. Cestodes and digenetic trematodes were placed in distilled water and allowed to relax and, in the case of the trematodes, to expel some of their eggs. They were fixed in hot alcohol-formalin-acetic acid (A.F.A) and stored in 70% ethyl alcohol. Standard histological techniques were followed in preparing permanent mounts of the Platyhelminthes. Stains used included Mayer's paracarmine, Semichon's carmine, and Grenacher's alcoholic borax-carmine.

Larger nematodes were immersed in boiling A.F.A., causing them to straighten instantly. Filamentous nematodes (Capillaria spp.) were allowed to relax and die in distilled water. The heligmosome nematodes were very difficult to uncoil for study. Murphy (1952) had similar difficulty when working with Longistriata neotoma. Although several different techniques for straightening these nematodes were undertaken, freezing was the most effective. Live worms were removed from the host and transferred to a petri dish containing tap water, which was placed in the freezer until the water had frozen. The dish was then removed, and the water was allowed to melt at room temperature. The majority of the males and a few females which underwent this treatment uncoiled at least to some degree.

Nematodes were stored in 50% or 70% ethanol. Carbohic acid (liquified phenol) was used to clear the worms for study. After examination, they were returned to the ethanol.



The data were analyzed using chi-square tests. Although it is frequently recommended with small sample sizes (Sokal and Rohlf, 1969), Yates' correction for continuity was not applied to the chi-square tests of independence. Apparently, Yates' correction is not necessary, even with sample sizes as low as 20 (Sokal and Rohlf, op. cit.).

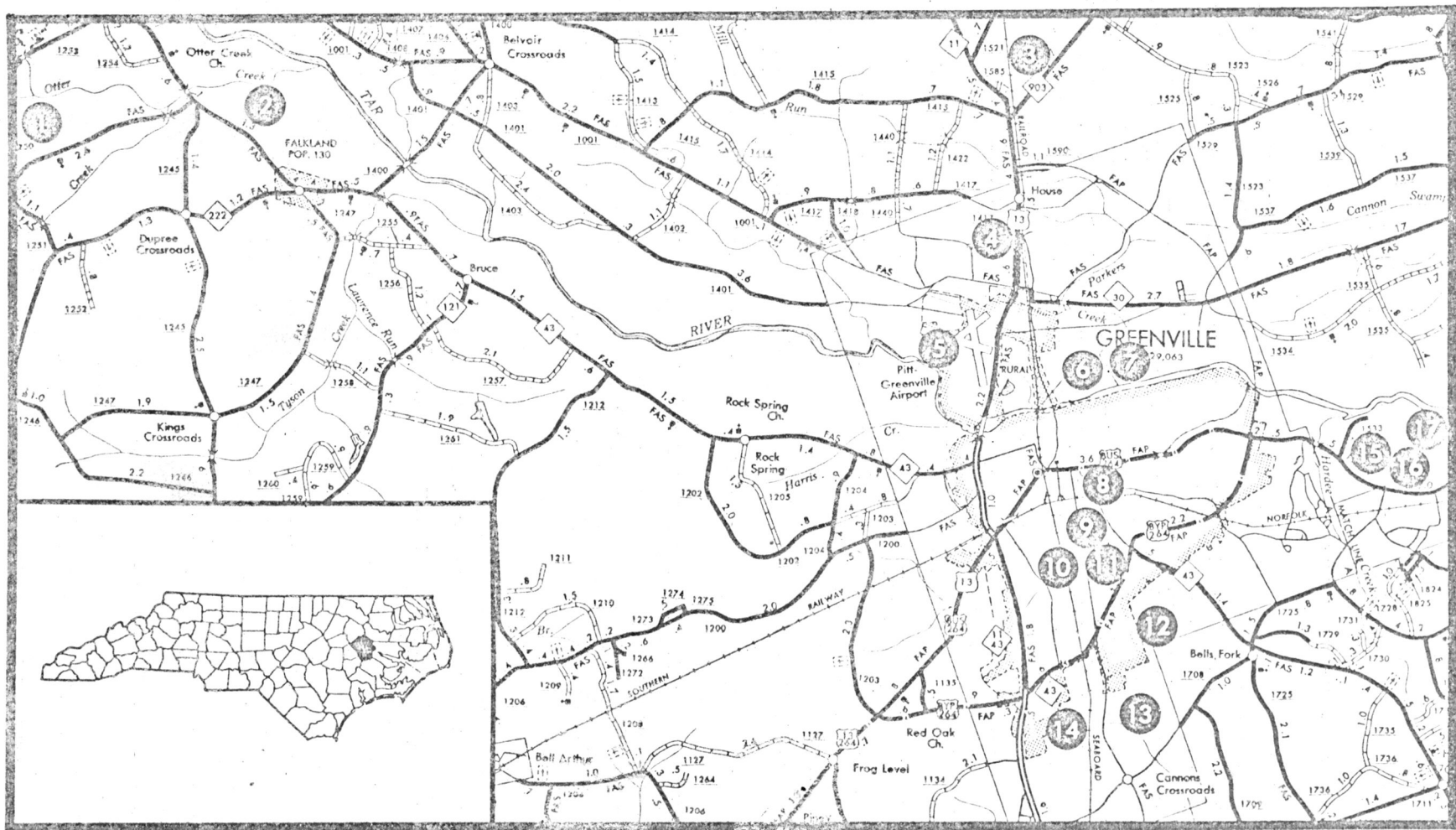


Figure 1. Location of collection sites in Pitt County, North Carolina.

## RESULTS

During a 17 month period from December, 1973, through April, 1975, small mammals were trapped in coastal plain woodlands. The 12,742 trap nights (one trap exposed for one night was counted as one trap night) yielded only 148 small mammals (Table I). Trap success, which was the number of small mammals taken per 100 trap nights, varied from approximately 2% during the winter and early spring to less than 0.5% during the warmer months of the year (June to September). Wood mice were collected during each month of the year, but the number of mice taken during the spring and summer was very small, as indicated by the percent of trap success during this period. Blarina brevicauda was captured only sporadically. Similar varying success in trapping mammals has been reported by numerous investigators.

Hassalstrongylus forresteri Durette-Desset, 1974 was recovered from the small intestine of one male (22) and one female (43) rice rat. This nematode has not been previously reported from North Carolina. The only other helminth found to be infecting O. palustris was a single larval nematode encysted beneath the visceral peritoneum of the intestine of the female.

One of the two house mice examined harbored 62 cecal nematodes which were identified as Aspicularis sp. Schulz, 1924. This was the only species of endoparasite recovered

from Mus musculus.

Eleven species of helminths representing three phyla and four classes were identified from the short-tailed shrews examined (Table II). The nematodes Capillaria blarinae Ogren, 1953 and Porrocaecum americanum Schwartz, 1925 constitute new state records. Twenty-six (83.1%) of the shrews were hosts for one or more species of internal parasites. Multiple infections were common. One shrew (3.9%) was infected with five species of helminths, two (7.7%) with four species, 11 (42.3%) with three species, six (23.1%) with two species, and six (23.1%) with one species. The nematodes C. blarinae and Porrocaecum encapsulatum Schwartz, 1925 were by far the most prevalent helminths, occurring in 48.4% and 35.5% of the shrews, respectively. The remaining helminths occurred in a small percentage of hosts.

The degree, level, or intensity of infection (parasite load or burden), expressed as the number of parasites per infected host, was low for all the helminths in B. brevicauda except P. encapsulatum, which occasionally occurred in comparatively large numbers. Differences in the prevalence (percent occurrence) and intensity of infection with helminths were observed relative to the sex of the host. Although male shrews tended to be more frequently infected with parasites than females, the worm burdens of females were slightly larger than those of males (Table II).

However, these differences were not found to be significant when tested with the chi-square ( $P > .1$ ). The relatively small sample of B. brevicauda did not permit determination of the effect of sex on the recruitment and establishment of the various species of helminths.

A search of the literature revealed only three prior studies which considered the total endoparasite fauna of B. brevicauda. Their results and those of the present study are summarized in Table III. The differences in the number and variety of endoparasites reported by the authors are probably the consequence of three factors: the examination of a small sample of shrews, cursory autopsy methods, and a limitation in the occurrence of the intermediate host. The data from these surveys provide an almost complete list of the known helminths comprising the endoparasite population of the short-tailed shrew.

Fifty-two (46%) of the wood mice were found to harbor six species of endoparasites (Table IV). All of these species have been recovered from wood mice taken in piedmont North Carolina or nearby states with the exception of Boreostrongylus peromysci Durette-Desset, 1974. This nematode has been described from the Florida mouse (Peromyscus floridanus) and the cotton mouse (Peromyscus gossypinus) in Florida (Durette-Desset, 1974).

The majority of the helminth infections (73.1%) involved only a single species; multiple infections were

rare. In addition, P. leucopus showed low prevalence and infection levels for all parasites except Capillaria americana Read, 1949 and Boreostrongylus peromysci. These were the only helminths which occurred frequently enough to determine the extent to which their prevalence and degree of infection of P. leucopus was influenced by the sex and age of the host and the season of the year.

Although C. americana was found to occur most frequently in male wood mice, female P. leucopus were usually more heavily infected (Table V). When the total helminth fauna was considered, these same trends held. However, these differences between the sexes were not found to be significant in either case ( $P > .1$ ).

Conversely, Boreostrongylus peromysci was recovered from females slightly more often than from males, and infected males had larger worm burdens than the females. Once again, these differences fell far short of the 5% significance level.

Differences in the composition of the helminth fauna of male and female hosts were observed. The endoparasite population of the female wood mice was comprised entirely of two helminths C. americana and Boreostrongylus peromysci. In addition to these two nematodes, four other helminths Brachylaima peromysci Reynold, 1938, Entosiphonous thompsoni Sinitsin, 1931, Capillaria hepatica (Bancroft, 1893), and an encysted larval nematode were found in male hosts.

The prevalence and intensity of helminth infections in wood mice of two age classes are given in Table VI. Adults were individuals which had reached an age of approximately 40 to 50 days or more and were undergoing or had completed the post-juvenile molt. Juveniles included those mice which were completely in juvenile pelage and consequently were less than 40 to 50 days old.

The degree of infection of P. leucopus with helminths was higher among the adults than the juveniles, a difference due chiefly to C. americana and Boreostrongylus peromysci, which exhibited a higher mean worm burden in the adult hosts. These differences did not approach the 5% significance level.

Adult wood mice were found to be more frequently infected with endoparasites than the juveniles, which exhibited a relatively low rate of infection (18.2%). Capillaria americana occurred in only a single juvenile wood mouse, whereas 37.4% of the adults harbored this nematode. Boreostrongylus peromysci was also more prevalent among the adults than the juveniles, but this difference was not nearly as pronounced.

When tested for independence, the age differences in the prevalence of C. americana and all helminths considered together were highly significant ( $P < .005$ ). However, the difference in the prevalence of Boreostrongylus peromysci among the two age classes was not significant ( $P > .1$ ).

In addition to being considerably larger, the endoparasite population of the adult wood mice was also found to be more varied than that of the juvenile mice. Although C. americana and Boreostrongylus peromysci made up the major portion of the parasite load of the adult hosts, two trematodes Brachylaima peromysci and E. thompsoni and two other nematodes C. hepatica and an encysted larval nematode occasionally occurred. On the other hand, the parasite load of the juvenile mice was comprised almost totally of Boreostrongylus peromysci. Only one of the 22 juveniles examined was infected with another internal parasite C. americana.

The data on the prevalence and intensity of infections of P. leucopus with C. americana and Boreostrongylus peromysci were combined into periods corresponding to the four seasons of the year (Figs. 2,3). These data demonstrate that the number of wood mice infected with either C. americana or Boreostrongylus peromysci were not uniformly distributed in all seasons. Boreostrongylus peromysci was most prevalent among wood mice in the spring and least abundant in the summer and fall. C. americana occurred most frequently during the fall and least frequently in the spring. Seasonal trends in the prevalence of the total helminth population follow those of C. americana. Although the data are suggestive of a seasonal difference, chi-square values did not exceed the 5%



significance level.

Seasonal trends in the degree of infection of P. leucopus with C. americana and Boreostrongylus peromysci are similar to those seen for the prevalence of these worms. Infection with Boreostrongylus peromysci was highest in the spring and summer and lowest in the fall and winter (Fig. 3). Again, these differences were not significant ( $P > .1$ ).

Seasonal changes in the intensity of C. americana infections were highly significant ( $P < .005$ ) when compared with values calculated on the basis of the assumption of equally intense infections in all seasons. Heaviest infections were during the summer and fall; spring was a period of light infection (Fig. 2).

Pregnant P. leucopus were captured during January (1), February (2), March (5), May (1), October (2), and November (1). The endoparasite population of these pregnant females was compared with that of non-pregnant females in an attempt to determine if pregnancy of the host influenced the prevalence or intensity of infections (Table VII).

Capillaria americana and Boreostrongylus peromysci were the only helminths found in female wood mice. These helminths occurred in both pregnant and non-pregnant individuals but with greater frequencies in pregnant females. When tested for independence, neither of these differences was significant at the 5% level. However, the difference in the

prevalence of Boreostrongylus peromysci among pregnant and non-pregnant females did approach close enough to statistical significance ( $.1 > P > .05$ ) to suggest a relationship with pregnancy. The data for the combined prevalence of these two helminths among the two types of females were statistically significant ( $.025 > P > .01$ ). The parasite loads of the pregnant and non-pregnant wood mice were not significantly different.

Table I

Small Mammals Trapped in Wooded Areas  
of Pitt County, North Carolina

Species	Number Captured	
	Male	Female
<u>Peromyscus leucopus</u>	72	41
<u>Blarina brevicauda</u>	14	17
<u>Oryzomys palustris</u>	1	1
<u>Mus musculus</u>	2	0

Table II

The Occurrence of Helminths in 31 Blarina brevicauda by Sex

Parasite	Male				Female				Total			
	Examined:		14		Examined:		17		Examined:		31	
	Infected:		13		Infected:		13		Infected:		26	
	No. Hosts Infected	Total No. Helminths	Helminths per Infected Host		No. Hosts Infected	Total No. Helminths	Helminths per Infected Host		No. Hosts Infected	Total No. Helminths	Helminths per Infected Host	
			Mean	Range			Mean	Range			Mean	Range
Acanthocephala:												
<u>Centrorhynchus</u> <u>conspicuosus</u>	1	5	5.0	5	2	3	1.5	1-2	3	8	2.7	1-5
Cestoda:												
<u>Hymenolepis</u> <u>acanthocephalus</u>	3	22	7.3	6-12	1	2	2.0	2	4	24	6.0	2-12
Nematoda:												
<u>Capillaria</u> <u>blarinae</u> *	8	33	4.1	3-9	7	49	7.0	2-15	15	82	5.5	2-15
<u>Capillaria</u> <u>hepatica</u> **	0	0	0.0	0	2	---	---	---	2	---	---	---
<u>Capillaria</u> <u>plica</u>	2	6	3.0	2-4	3	9	3.0	1-6	5	15	3.0	1-6
<u>Porrocaecum</u> <u>americanum</u> *	2	3	1.5	1-2	1	8	8.0	8	3	11	3.7	1-8
<u>Porrocaecum</u> <u>encapsulatum</u>	4	48	12.0	1-33	7	54	7.7	1-14	11	102	9.3	1-33
<u>Physaloptera</u> sp.	3	8	2.7	1-5	1	3	3.0	3	4	11	2.8	1-5
Trematoda:												
<u>Brachylaima</u> <u>rhomboides</u>	4	8	2.0	1-3	2	18	9.0	6-12	6	26	4.3	1-12
<u>Entosiphonius</u> <u>thompsoni</u>	2	3	1.5	1-2	1	10	10.0	10	3	13	4.3	1-10
<u>Panopistus</u> <u>pricei</u>	2	3	1.5	1-2	3	4	1.3	1-2	5	7	1.4	1-2
Total:	13	139	10.7	2-41	13	160	12.3	1-32	26	299	11.5	1-41

\*North Carolina is a new locality for species

\*\*Presence of C. hepatica was indicated solely by the recovery of eggs

Table III

Comparison of Present Study with Previous Studies of the Helminth Fauna of Blarina brevicauda

Helminth	North Carolina Present Study	North Carolina Miller et al., 1974	Massachusetts Boyd and Dunning, 1960	Ohio Oswald, 1958
Acanthocephala:				
<u>Centrorhynchus</u> <u>conspectus</u>	X			X
<u>Centrorhynchus</u> sp.		X		
Cestoda:				
<u>Hymenolepis</u> <u>anthocephalus</u>	X	X	X	X
<u>Hymenolepis</u> <u>blarinae</u>			X	X
<u>Hymenolepis</u> sp.			X	X
<u>Pseudodiorchis</u> <u>reynoldsi</u>				X
<u>Protogynella</u> <u>blarinae</u>			X	X
<u>Protogynella</u> <u>pauciova</u>			X	X
Trematoda:				
<u>Brachylaima</u> <u>rhomboideus</u>	X	X*	X	X
<u>Entosiphonus</u> <u>thompsoni</u>	X	X		X
<u>Panopistus</u> <u>pricei</u>	X	X	X	X
<u>Corrigia</u> sp.			X	
<u>Brachylecithum</u> sp.		X		
Nematoda:				
<u>Angiostrongylus</u> <u>blarini</u>				X
<u>Capillaria</u> <u>blarinae</u>	X		X	X
<u>Capillaria</u> <u>hepatica</u>	X			
<u>Capillaria</u> <u>pilica</u>	X	X		
Encysted larval anisakids			X	
<u>Longistriata</u> <u>depressa</u>		X		X
<u>Parastrongyloides</u> <u>winchesi</u>				X
<u>Physaloptera</u> <u>limbata</u>				X
<u>Physaloptera</u> sp.	X	X		
<u>Porrocaecum</u> <u>americanum</u>	X		X	X
<u>Porrocaecum</u> <u>encapsulatum</u>	X	X	X	X
<u>Porrocaecum</u> <u>ensicaudatum</u>				X

\*Reported as Brachylaima dolichodigitus, a synonym for B. rhomboideus (Villegla, 1953b)

Table IV

Total Number of Helminths from 113 Peromyscus leucopus by Sex and Age of the Host and Season of the Year

Host	Winter (Dec.-Feb.)				Spring (Mar.-May)				Summer (June-Aug.)				Fall (Sept.-Nov.)				Total			
	J		A		J		A		J		A		J		A		J		A	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Examined:	6	10	31	13	4	3	18	8	0	0	5	2	1	0	7	5	10	12	56	27
Infected:	2	1	20	6	0	0	6	6	0	0	3	0	1	0	4	3	3	1	30	14
Parasite																				
<u>Capillaria</u> <u>americana</u> <sup>a</sup>	15	0	171	95	0	0	66	31	0	0	67	0	0	0	16	124	15	0	320	250
<u>Boreostrongylus</u> <u>peromysci</u> <sup>a,b</sup>	10	8	36	10	0	0	61	39	0	0	11	0	1	0	0	7	11	8	108	56
<u>Brachylaima</u> <u>peromysci</u> <sup>a</sup>	0	0	2	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	12	0
<u>Entosiphonous</u> <u>thompsoni</u>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<u>Capillaria</u> <u>hepatica</u> <sup>c</sup>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	---	0	0	0	---	0
Encysted larval nematode	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0
Total	25	8	217	105	0	0	127	70	0	0	78	0	1	0	26	131	26	8	448	306

<sup>a</sup> North Carolina is a new locality for species<sup>b</sup> New host record for parasite<sup>c</sup> Presence of C. hepatica was indicated solely by the recovery of eggs

J=Juvenile

A=Adult

M=Male

F=Female

Table V

The Occurrence of Parasites in Each Sex of Peromyscus leucopus

Parasite	Male - 72		Female - 41	
	Percent Infected	Mean no. per Infected Host	Percent Infected	Mean no. per Infected Host
<u>Capillaria americana</u>	33.3	14.0	26.8	22.7
<u>Boreostrongylus peromysci</u>	20.8	7.9	22.0	7.1
Total Helminths	50.0	13.8	39.0	19.6

Table VI

The Occurrence of Parasites in Juvenile and Adult Peromyscus leucopus

Parasite	Juvenile - 22		Adult - 91	
	Percent Infected	Mean no. per Infected Host	Percent Infected	Mean no. per Infected Host
<u>Capillaria americana</u>	4.6	15.0*	37.4	16.8
<u>Boreostrongylus peromysci</u>	13.6	6.3	23.1	7.8
Total Helminths	18.2	8.5	52.8	16.2

\*number recovered from a single host



Table VII

The Occurrence of Parasites in Pregnant and Non-pregnant

Female Peromyscus leucopus

Parasite	Pregnant - 12		Non-pregnant - 29	
	Percent Infected	Mean no. per Infected Host	Percent Infected	Mean no. per Infected Host
<u>Capillaria americana</u>	41.7	23.4	20.7	22.2
<u>Boreostrongylus peromysci</u>	41.7	7.8	13.8	6.25
Total Helminths	66.7	19.5	38.1	19.7

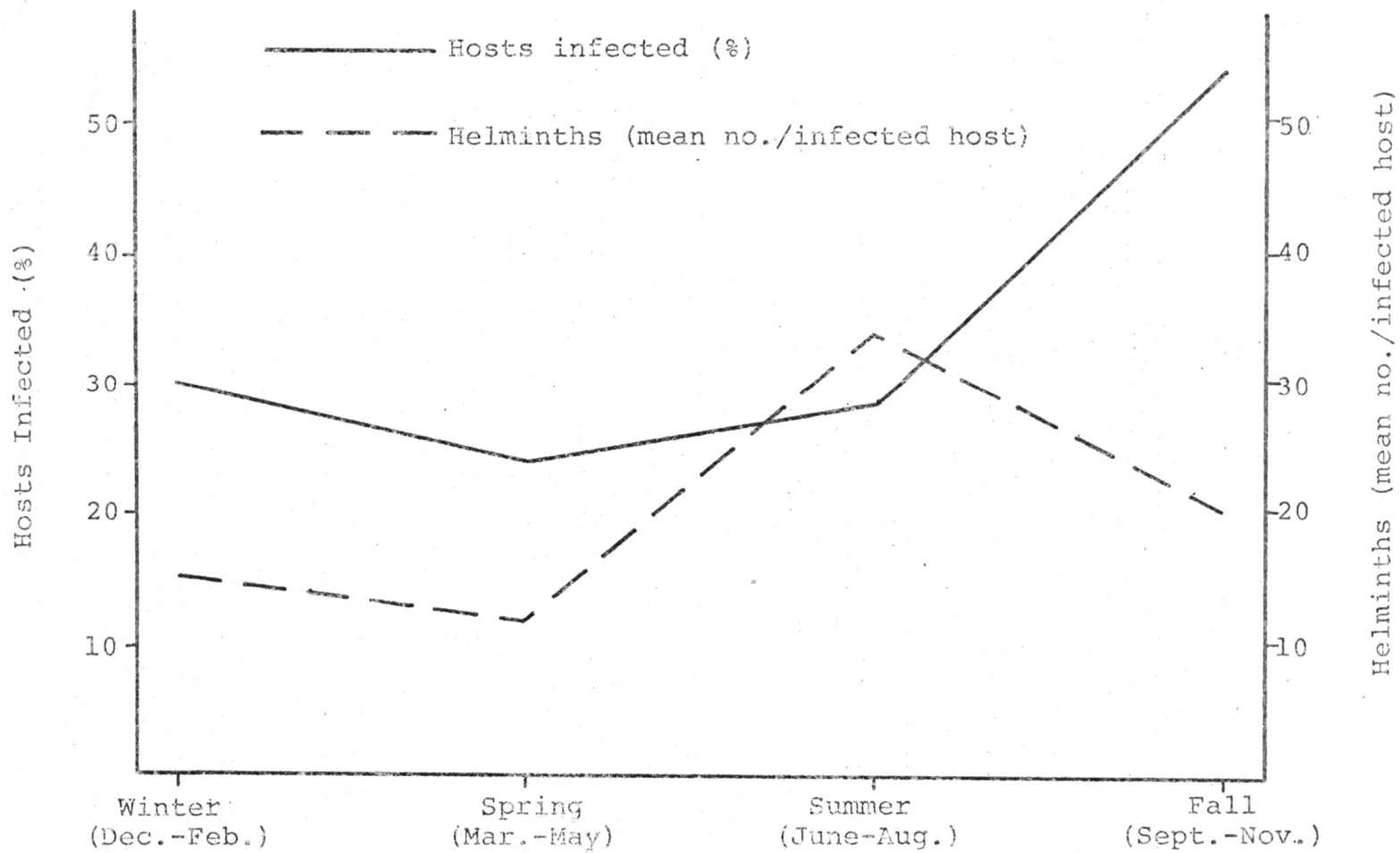


Figure 2. Seasonal Occurrence of Capillaria americana in Peromyscus leucopus.

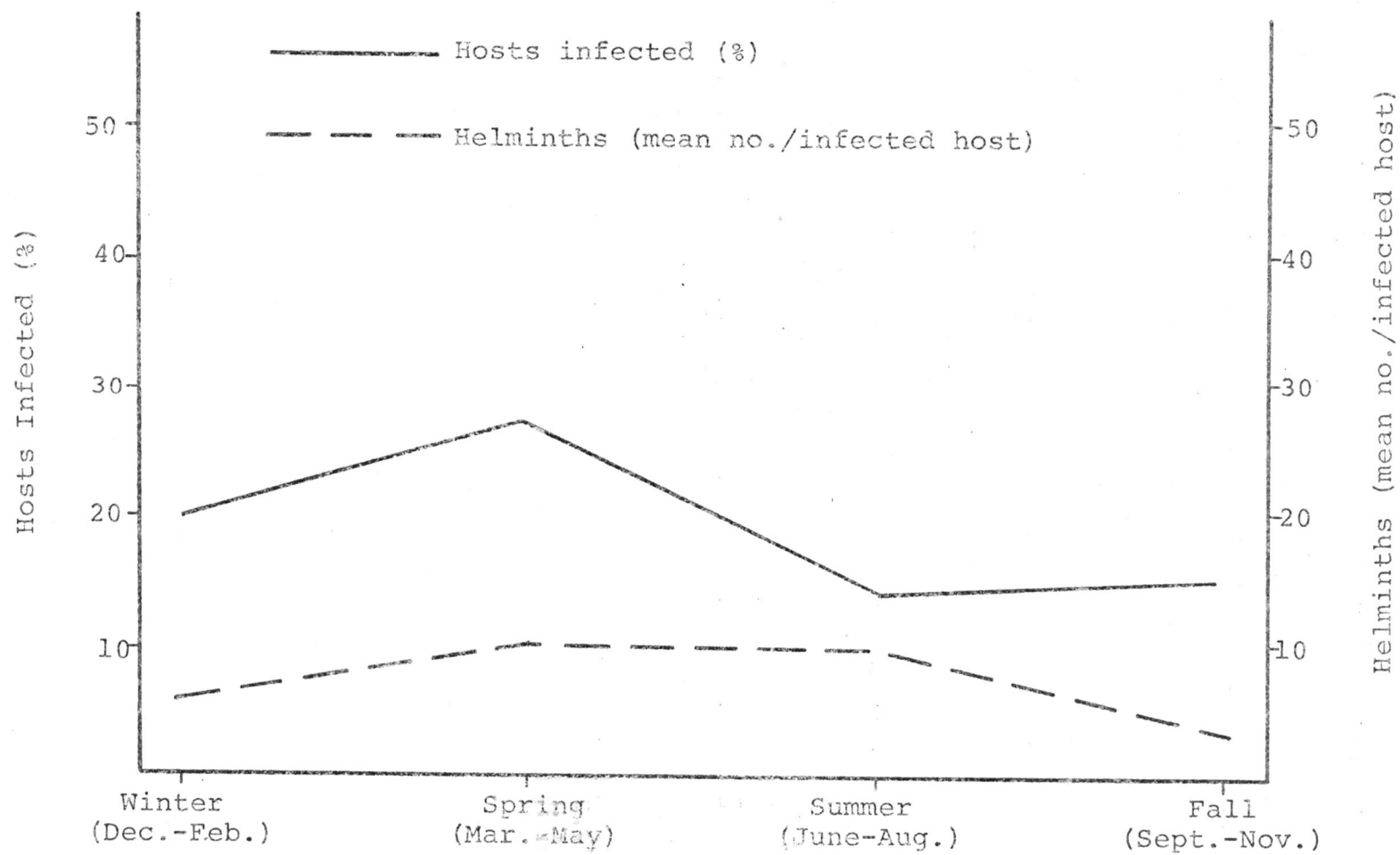


Figure 3. Seasonal Occurrence of Hareostromylus peromysci in Peromyscus leucopus.

## DISCUSSION

The overall poor trapping success experienced during this investigation is indicative of a low population of small woodland mammals in this area. The almost complete failure in trapping small mammals during the summer and early fall may largely reflect seasonal fluctuations in the population levels of P. leucopus. Wood mouse population density in the South is generally at a low point during the late summer or early fall as a result of diminished reproductive activity in the summer (Stickel and Warbach, 1960). The poor success during these seasons may also be attributed to changes in bait acceptability and attractability when natural foods are abundant (Fitch, 1954).

The low population densities are apparently characteristic of much of this region. Paul and Cordes (1969) had similar success (approximately 3%) in trapping P. leucopus in the coastal plain of North Carolina (personal communication from J.G. Boyette, Department of Biology, East Carolina University, Greenville, N.C.). Gore (1967) found small mammal populations to be low in several habitats in the South Carolina coastal plain. It seems that much of the coastal plain is generally unfavorable for small mammals due to the wet habitats or the periodic flooding characteristic of much of the region (personal communication from P.D.

Weigel, Department of Biology, Wake Forest University, Winston-Salem, N.C.). The adverse effects of flooding on small mammal populations have been noted by several authors (Blair, 1939; Turner, 1966; Wetzel, 1958).

Although small mammals were scarce in all the woodland habitats trapped, the fewest numbers were observed in pure pine forests. The population increased in those communities in which hardwoods had assumed dominance. A similar pattern has been noted during other investigations into the relative abundance of mammals in plant communities of the southeastern United States (Golley et al., 1965; McKeever, 1959).

Since a large proportion of the small mammal fauna of the coastal plain consists of herbivores or granivores (Golley et al., *op. cit.*), population size should be strongly influenced by the vegetative changes that occur in old field succession. Smaller mammals are most common in the preforest stage of community development (Golley et al., *op. cit.*), when the amount of plant matter available to ground-dwelling animals is maximum. However, as pines replace the herbaceous annuals and perennials and assume dominance in the overstory and understory strata, the production of food suitable for many small mammals declines dramatically. Therefore, pine forests support the smallest mammalian population. As the pine stand matures, hardwoods dominate first the understory and finally the overstory when

a climax community becomes established. The number of species of shade-tolerant shrubs, vines, and herbs in the understory stratum also increases as succession progresses (Oosting, 1942). Consequently, there should be a corresponding rise in production of herbage, seeds, nuts, acorns, and fleshy fruits that are important food items of several small forest mammals (Hamilton, 1941). This difference in food availability between pine-dominated stands and climax oak-hickory deciduous forests may be largely responsible for the latter's ability to support a larger mammalian population. Getz (1961b) found that the presence of a stable year-round food supply in oak-hickory habitats was a major factor enhancing the number of wood mice there. However, the distribution of the insectivorous shrew is primarily influenced by moisture availability, because the shrew is unable to regulate evaporative losses (Getz, 1961a).

According to McKeever (1959), current land practices in the South are resulting in an increase in pine forests. The cultivation of many drier coastal plain sites further reduces the habitat suitable to most small mammals (personal communication from P.D. Weigel). These trends may be expected to continue to reduce the populations of some small mammals.

A considerable variety of endoparasites were recovered despite the small host populations, confined to limited

habitats. The pinworms recovered from one of the two house mice necropsied appear to belong to the genus Aspicularis, which contains approximately 10 species occurring in various rodents (Levine, 1968). Positive identification was impossible because no males were recovered. This is the first report of a nematode belonging to this genus from North Carolina.

Hassalstrongylus forresteri was initially reported by Durette-Desset (1972) as Hassalstrongylus musculi (Dikmans, 1935) from the small intestine of a Florida rice rat. After examining the type specimens of H. musculi, Durette-Desset (1974) found that H. forresteri differed in the following respects: the genital cone is not hypertrophied, the terminal ends of the two spicules are enlarged and identical to each other, and the spicules are smaller. In addition to H. forresteri, two other heligmosome nematodes belonging to this genus have been described from the small intestine of O. palustris (Durette-Desset, 1974). These other species have not been recovered from North Carolina hosts.

The endoparasitic population of B. brevicauda was considerably larger and more varied than those of the other small mammals (Table II). Three Trichurids C. blarinae, C. hepatica, and Capillaria plica (Rudolphi, 1819) were among the five species of nematodes identified from the shrews examined. Capillaria blarinae was originally described by Ogren (1953) from B. brevicauda taken in

Illinois. It has since been recovered from short-tailed shrews in Ohio (Oswald, 1958) and Massachusetts (Boyd and Dunning, 1960). This species occupies tunnels in the esophageal epithelium. Unlike several other members of the genus, C. blarinae exhibits considerable host specificity. Blarina brevicauda is the only host from which it has been recorded (Yamaguti, 1961).

Conversely, C. hepatica and C. plica have been found to occur in a variety of hosts, including man in the case of the former (Yamaguti, op. cit.). Capillaria hepatica infests the liver of its hosts, where it causes yellowish lesions which may be small and widely scattered, or continuous and involving all the hepatic lobes (Luttermoser, 1938). The parasite's presence may be verified by the recovery of the characteristic two-plugged eggs from the liver parenchyma (Freeman and Wright, 1960). Infection occurs by ingesting fully developed eggs, freed from the liver by death and decomposition of the host or when the host is eaten by another animal (Olsen, 1974).

This is only the second report of C. hepatica from B. brevicauda. The initial recovery was made by Solomon and Handley (1971). They found three of 133 short-tailed shrews captured in the Appalachian Mountains of Virginia infected with this helminth.

Capillaria plica is an inhabitant of the urinary bladder of various carnivorous mammals (Miller and Harkema,



1968). It utilizes several different species of earthworms as intermediate hosts. Infection of the definitive host takes place when earthworms harboring first stage larvae are eaten (Olsen, 1974). It is curious that C. plica has only been found to occur in North Carolina short-tailed shrews (Miller et al., 1974; present study). This nematode should probably be ubiquitous among Blarina, because earthworms form an important part of their diet (Hamilton, 1941; Whittaker and Ferraro, 1963).

The larval nematodes P. americanum and P. encapsulatum were present throughout the body cavity of 14 B. brevicauda in cysts attached to the mesenteries and the peritoneum. On a few occasions, P. americanum was recovered from subcutaneous cysts. The adult stages of these two nematodes have not been described but are presumed to occur in birds of prey, such as hawks and owls (Schwartz, 1925).

A small number of sexually immature nematodes identified as Physaloptera sp. Rudolphi, 1819 were removed from the stomachs of four short-tailed shrews. No males were found among the nematodes recovered. Miller et al. (op. cit.) also reported immature specimens of this genus from two shrews. It is probable that the occurrence of these nematodes in B. brevicauda represents accidental infections.

Digenetic trematodes occurred in a relatively high percentage (32.3%) of the shrews captured. The population

of digeneans was comprised of Brachylaima rhomboideus (Sinitsin, 1931), E. thompsoni, and Panopistus pricei Sinitsin, 1931, all of which inhabit the lumen of the intestine. All three of these brachylaemid trematodes utilize land snails as the first and second intermediate hosts (Krull, 1934, 1935; Villella, 1953a, 1953b). Blarina becomes infected by eating snails which contain infective metacercaria. The comparatively high prevalence of infections with these digeneans may be explained by the fact that a variety of terrestrial molluscs are frequently eaten by short-tailed shrews (Ingram, 1942; Whittaker and Ferraro, 1963).

Hymenolepis anthocephalus Van Gundy, 1935 was the only representative of the class Cestoidea found in B. brevicauda. It is the only cestode recorded from shrews taken in North Carolina (Miller et al., 1972; present study). According to Oswald (1958), six other species of tapeworms have been reported from this host in other localities. The failure to recover any of these other species in North Carolina may indicate a limitation in the distribution of the arthropod intermediate hosts of many of these cestodes.

Van Gundy (1935) recovered a cysticeroid larva of H. anthocephalus, encysted in a piece of Elateridae larvae, from the intestinal contents of a shrew. The larval beetle may be serving as an intermediate host for this helminth

species. Evidently, H. anthocephalus is restricted in occurrence to Blarina (Rausch and Kuns, 1950; Yamaguti, 1959).

A small number of juvenile acanthocephalans (cystacanth) identified as Centrorhynchus conspectus Van Cleave and Pratt, 1940 were found encysted in the mesenteries or the liver of three shrews. In addition, a juvenile of this species, which had lost its sheath and evaginated its proboscis, was found free in the intestine of one host. Apparently, the shrew had just consumed an invertebrate acting as an intermediate host for this helminth, and the cystacanth had not had time to migrate from the gut into the body cavity and encapsulate. The adult stage of C. conspectus has been reported from a barred owl, Strix varia varia, taken in North Carolina (Van Cleave and Pratt, 1940). Although the life history is not known, it is probably similar to the basic pattern exhibited by all acanthocephalans (Noble and Noble, 1964; Olsen, 1974). The first intermediate hosts of this group of worms have almost invariably been found to be arthropods (Nicholas, 1967; Olsen, op. cit.). The acanthocephalid larva, an acanthor, hatches from the egg within the arthropod and develops first into the acanthella and then into a cystacanth several weeks later (Cheng, 1973). Infection occurs when the cystacanth is ingested by a potential definitive host. In some vertebrates, the cystacanth may not be able to develop to

sexual maturity, and it migrates from the gut into the body cavity and encysts. Such vertebrates may serve as carrier hosts (i.e. paratenic hosts), depending on the feeding habits of the definitive host (Nicholas, 1967). This is the status of the short-tailed shrew in the life history of C. conspectus. When a carrier host is eaten by another carrier host animal, the cystacanth is transferred into the second carrier host and survives without losing its ability to develop into an adult (Dogiel, 1964). The definitive host S. varia varia can become infected by ingesting the arthropod intermediate host or a carrier host, such as Blarina (Cheng, 1973; Dogiel, op. cit.). However, the barred owl exhibits a carnivorous mode of life (Bent, 1938) and is more likely to be infected by ingesting a small insectivorous animal than by eating an intermediate host.

Encapsulated cystacanths belonging to the genus Centrorhynchus have been recovered from a wide variety of animals including several species of Salientia (Rana catesbeiana, Rana sphenoccephala, Bufo fowleri, Pseudacris brimleyi, Hyla crucifer) (Brandt, 1936) and a bobcat, Lynx rufus (Miller and Harkema, 1968). Hosts, such as the bobcat, that have food links to the invertebrate intermediate host through Blarina and other small animals, but not to the definitive host, represent a blind-end in the life cycle.

Collins (1969) recovered C. conspectus from cysts in

many eastern North Carolina water snakes (Natrix spp.) and a few water moccasins (Agkistrodon piscivorus piscivorus). He found the rate of infection of Natrix sipedon and Natrix erythrogaster with C. conspectus to be quite high. It is probable that many frogs, which are important food items of these two water snakes (Laughlin, 1959), are also acting as carrier hosts for this helminth.

Insectivorous animals like the terrestrial shrew, which avoids standing water (Getz, 1961a), and semiaquatic or aquatic frogs seem to be serving as carrier hosts for C. conspectus. The intermediate host for this helminth may be a terrestrial or flying insect with an aquatic stage in its life history. These carrier host animals have positions in the food chain that would greatly facilitate the infection of the barred owl.

The wood mouse, P. leucopus, consistently exhibited a range and prevalence of helminth infections much lower than those seen in B. brevicauda. This is certainly correlated with differences in the diets of these two small mammals. The wood mouse has been found to ingest primarily plant material (Calhoun, 1941; Cogshall, 1928; Whittaker, 1966), whereas the feeding habits of the shrew are generally considered insectivorous (Hamilton, 1930, 1941). The direct relationship between the abundance of invertebrates in the diet and the number of species and the intensity of infections with helminths, particularly trematodes and

cestodes, can be attributed to the fact that these parasites utilize invertebrate intermediate hosts (Dogiel, 1964). Furthermore, the small number of helminth species occurring in P. leucopus and the low prevalence of the infections, relative to that seen in Blarina, may also be accredited to the semi-arboreal mode of life of the wood mouse. Dogiel (op. cit.) states contact with the soil is closely associated with infection by many parasites, either directly, when the host eats their eggs or larvae with its food, or indirectly, through the intermediate hosts inhabiting the soil or vegetation. The short-tailed shrew, unlike the wood mouse, is generally terrestrial (Barbour and Davis, 1974) and, consequently, spends much more time on or under the soil. As a result, its infection with helminths is correspondingly greater.

Although nematodes almost totally comprised the helminth fauna of P. leucopus, two digenetic trematodes E. thompsoni and Brachylaima peromysci did occur (Table IV). Entosiphonous thompsoni was the only helminth other than C. hepatica found to infect both Blarina and P. leucopus. A single worm was recovered from the intestine of an adult wood mouse. Several Brachylaima peromysci (six average) also occurred in the intestine of two adult males. The life cycle of Brachylaima peromysci is not known; it is probably analogous to the life cycles of other species of Brachylaemidae, such as those of the digeneans infecting

Blarina. Although the general food habits of P. leucopus are those of a herbivore, the presence of E. thompsoni and Brachylaima peromysci suggests a more omnivorous diet.

Four species of nematodes were harbored by the wood mice examined. Only two of these C. americana and Boreostrongylus peromysci occurred to any significant degree. Only one adult male was infected with C. hepatica, whereas two contained some encysted larval nematodes. The seven unidentified larval nematodes occurred in very small cysts approximately 500 to 600 microns in diameter, attached to the visceral peritoneum surrounding the stomach or intestine. These tiny nematodes were very similar to those taken from cysts in O. palustris during the present investigation and the larval nematodes described by Harkema (1936) from P. leucopus. It is possible that these are all the same species of nematode.

The data from this study suggest a low frequency of C. hepatica infections among small woodland mammals of this area. Some hosts for this parasite constitute a reservoir of infection to which humans may be exposed (Olsen, 1974). However, it is doubtful that Blarina and P. leucopus are an important source of C. hepatica infections in man, because these mammals rarely occur in his habitat.

Differences in the prevalence and level of infections of male and female wood mice were not great. However, males were infected with a broader range of helminths, including

two digeneans and two nematodes not seen in females (Table IV). The more extensive foraging habits of the males, which would increase their chances of encountering the infective larvae of helminths, could account for the greater variety.

The data show that the endoparasite fauna of P. leucopus undergoes change dependent upon the age of the host (Table VI). The number of helminth species, their prevalence, and the level of infection were all greater for older wood mice. These trends are not unusual. Dogiel (1964) concludes that the progressive growth of infestation with the age of the host holds for a number of host species, including fishes, birds, and mammals. The observed trends in the prevalence of helminths among juvenile and adult wood mice are due chiefly to the intestinal nematode C. americana, the most frequently encountered species in the sample. Boreostrongylus peromysci, unlike C. americana, was more evenly distributed between the two age classes (Table VI). Capillaria americana was rarely found in wood mice less than 40 to 50 days old, indicating that infection probably did not occur until after the young were weaned and had left the nest. Wood mice are weaned between 20 and 40 days of age, and the female abandons the litter soon afterwards (Nicholson, 1941). An increase in foraging and a change in feeding activities would be expected at this time. It appears that the greater susceptibility of older wood mice to C. americana infections is linked to a change in diet



that increases their chances of exposure to the infective larvae. A juvenile that consumes milk and a limited amount of solid matter is inaccessible to infection by many helminths, particularly those requiring an intermediate host to complete their life history. Although the life cycle of C. americana is not known, it is reasonable to assume that it includes an invertebrate intermediate host. This pattern is exhibited by several species of the family Trichuridae (Hyman, 1951; Olsen, 1974).

The relatively high prevalence of Boreostrongylus peromysci in juveniles suggests that nests may be an important source of infection for this helminth. Presumably, this intestinal inhabitant has a direct life cycle like other heligmosome nematodes studied. Infection has been found to occur either through the skin or orally (Durette-Desset, 1971; Skrjabin et al., 1954). Juvenile wood mice are probably especially susceptible to Boreostrongylus peromysci, considering the poor nest sanitation of the wood mouse. Nicholson (1941) has found that P. leucopus defecates within its nests, causing nests in continual use, such as family nests, to become foul. If the female harbors Boreostrongylus peromysci, many of the young are undoubtedly exposed to the infective stage before leaving the nest. Scott and Blynn (1952) found that a heligmosome nematode (Hassalstrongylus adunca) occurring in S. hispidus was always acquired by the young of heavily

infected females before they were weaned and left the nest. However, female wood mice with young are thought to frequently change the location of their nests (Nicholson, 1941). This may serve to restrict the occurrence of Boreostrongylus peromysci in juveniles by not allowing the infective larvae to accumulate in the nest. Young wood mice could also possess some degree of immunity, further limiting the frequency of nest acquired infections.

Seasonal changes were found to influence the prevalence and intensity of C. americana infections (Fig. 2). However, only the differences in the degree of infection of wood mice were statistically significant. In contrast, Boreostrongylus peromysci infections were more evenly distributed among wood mice throughout the year (Fig. 3). The occurrence of Boreostrongylus peromysci seems to be unaffected by changes in climate. This further suggests that this nematode is acquired in the nest, where external environmental conditions would be mitigated. The rare occurrence of the other internal parasites made it impossible to determine if there was seasonal variation in their distribution throughout the year.

It is difficult to speculate as to the causes of the seasonal trend in the intensity of C. americana infections, because its life history is unknown. However, if this nematode does utilize an invertebrate intermediate host to complete its developmental cycle, the occurrence of C.

americana in P. leucopus would be influenced by the biology of the invertebrate. Insects and other invertebrates are much more abundant in the late spring and summer than in other seasons. Wood mice would be more likely to ingest the intermediate host during this period; this may account for the rise in the intensity of infections during the summer (Fig. 2).

Another factor which may explain the seasonal distribution of C. americana infections is a change in the density and age composition of P. leucopus populations. The increase in the number of young wood mice in the winter and spring, resulting from a fall breeding season, probably contributes to the decrease in the level of infections with C. americana observed at this time. These mice are only a few months old and have had little time to encounter the infective stage. In the summer and early fall, wood mouse populations are smaller and primarily consist of older individuals. The intensity of C. americana infections would be high among these older adults, because they have had several months of high invertebrate activity in which to recruit the infective larvae. Elton et al. (1931) and Layne (1963) accredited seasonal trends in endoparasite abundance to changes in the age composition of the host population.

According to Dogiel (1964), seasonal changes in the parasite fauna are determined by many abiotic and biotic factors. These include climatic factors, changes in the

feeding habits and mode of life of the host that influence the probability of infection, the ecology of the intermediate host, and other factors. Certainly all of these contributed to the pattern of change observed for C. americana.

Pregnant wood mice were much more frequently infected with helminths than non-pregnant females (Table VII). This difference may have occurred because pregnant individuals are spending more time in the vicinity of the nest, which has been implicated as an important source of endoparasite infections because of fecal contamination. Hormones may also be responsible for this difference in susceptibility. Dobson (1961) has shown that hormonal changes in female laboratory rats are correlated with changes in resistance to infection with the nematode Nematospiroides dubius.

It appears that parasitism has little influence on the population dynamics of these small mammals. No individuals were encountered with overt signs of pathology that could be credited to internal parasites. The changes in the density of Peromyscus populations are probably largely a result of breeding pattern, environmental factors, and available food supply (McCarley, 1954). However, it is possible that low parasite loads, such as those encountered in this study, may adversely affect the host's physiology or behavior, resulting in increased susceptibility to predation or environmental stress (Layne, 1963).

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