

THESIS





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ECOLOGICAL ASPECTS OF A MAMMALIAN HOST-PARASITE SYSTEM

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By

Allan Christopher Carmichael

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

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ABSTRACT

ECOLOGICAL ASPECTS OF A MAMMALIAN HOST-PARASITE SYSTEM

By

Allan Christopher Carmichael

Field work was conducted in order to examine some of the ecological parameters involved in shaping and maintaining a naturally-occurring host-parasite system involving the helminth fauna of the meadow vole. Microtus pennsylvanicus. Special consideration was given to the blood fluke. Schistosomatium douthitti. Two questions were examined: (1) What is the spatial and temporal distribution of a parasite population within a host population? and (2) Does a parasite population affect a host population in terms of reproductive output? The data indicate that populations of voles living near water incur a higher parasite burden when compared with local populations of voles inhabiting drier upland sites. These parasite burdens differ both in composition and intensity. Differential reproductive output between voles from different habitat types was not clearly demonstrated. Data on host biology are brought to bear on an analysis of the host-parasite interaction as a coevolutionary system.



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INTRODUCTION

ALL PROPERTY.

Ecological aspects of parasitic interactions have long been neglected in deference to the more immediate concerns of disease control and prevention. Much information has been obtained relating to the impact of the environment upon parasitic life cycles. This information has been restricted largely to parasites of man and domestic mammals and a number of important syntheses have resulted, including those of MacDonald (1965), Crofton (1963) and Cohen (1977). Up until recently, most information concerning the ecology of parasites inhabiting wild mammals was derived from life-history studies and surveys of host populations. The recent expansion of the literature in this field reflects a growing awareness of the fact that a more complete understanding of the ecological aspects of parasitic relationships may lead to more effective control of these organisms and the diseases they produce (see Kennedy, 1975, and Kennedy, ed., 1976). This field of study has been characterized by Kennedy (1975:1) as follows: "Ecological animal parasitology is concerned with the distribution and abundance of parasites. This includes their distribution and abundance in space, in time and in



different hosts, and involves consideration of the factors regulating host-parasite interactions at both the individual and population level. It is above all concerned with the quantitative as well as qualitative relationships between parasites and their hosts."

In contrast with many parasitic relationships of importance to medical and veterinary research, parasites which occur in populations of wild mammals may not cause disease and debilitation. Harmful interactions may in many cases result from human perturbation. Naturally-occurring, host-parasite systems often appear to represent complex and somewhat stable coevolutionary systems in which detrimental effects on the individual host are minimized while the probability of parasite transmission is maximized.

The study of parasite population dynamics is often complicated by the life cycles of many of these organisms. Regulation of population growth occurs both as a result of biotic interactions as well as environmental impact upon free living stages. Many recent studies concerned with parasite ecology have focused upon parasites of ectothermic host organisms in which competition for resources and environmental variability are assumed to be the major forces limiting population growth. Mammalian systems, on the other hand, present a particularly complex situation due to the greater ability of most mammals to respond immunologically to parasites and to some extent regulate



the levels of parasitic infection. The intensity of response may vary from host to host as well as within the lifetime of a single host, making mammalian host-parasite systems particularly difficult to model. Nonetheless, the examination of naturally-occurring host-parasite systems may give some indication of the selective pressures involved in shaping these highly coordinated systems. Insight which will aid in determining the ecologically significant parameters involved in maintaining such systems may also be obtained.

The present study examined a specific naturallyoccurring host-parasite system in southcentral Michigan consisting of the helminth fauna of the meadow vole. Microtus pennsylvanicus. The blood fluke, Schistosomatium douthitti, was chosen for an analysis of ecologically important factors for two reasons. First, Zajac (1978) reported high levels of infection by this species in vole populations from the study areas during the two years previous to this study. Second, extensive reports have been published concerning the biology of this species and its role as a laboratory research organism. In the present study, two questions were examined: (1) Does the local distribution of a host population influence the composition and prevalence of its parasite fauna? and (2) Does a naturally-occurring parasite population affect its host population in terms of reproductive output? The parasite



faunas and demographic characteristics of vole populations from two distinct habitat types were contrasted in an attempt to answer these questions. The extremely large number of studies in the literature concerning the biology of the meadow vole can aid in interpreting population phenomena observed in this study and help to define the nature of parasitic impact upon vole biology.

Parasitic organisms have been implicated as causal agents in influencing microtine population fluctuations (Christian, 1963; Christian and Davis, 1964; Chitty, 1952; and Christian, 1961). Particular attention has been given to the brain protozoan, Frenkelia (= Toxoplasma) microti, although no definite correlations have been demonstrated between the occurrence of this parasite and any influence upon microtine population fluctuations (Findlay and Middleton, 1934, and Jellison, 1971). The interplay of stress due to crowding and increased susceptibility to parasitic infection has been examined by a number of authors (Davis and Read, 1958; Jackson and Farmer, 1970; Patterson and Vessey, 1973). Recent work by Seed and his colleagues (Seed et al., 1976, and Seed et al., 1978) has demonstrated that splenomegaly may be used as an indication of parasitic infections in wild voles. Their hypothesis that parasitism could lead to decreased reproductive potential has refocussed attention on the role of parasitic infection in microtine population declines. Wiger



(1977) attempted, primarily through a synthesis of available literature, to relate the effects which endoparasites have upon their hosts to models of population dynamics of <u>Microtus agestis</u>. The author provides a valuable literature review, but the speculative conclusions can only be applied to natural situations with caution.

Other parasites of microtine rodents have received attention in the literature, although their role in microtime population fluctuations has not been examined for the most part. Prominent among these are a variety of blood and digestive tract protozoans which have been studied by a number of authors (Baker et al., 1963; Fay and Rausch, 1969; Elton et al., 1931; and Cox, 1970). Also, in an interesting series of papers, Kisielweska (1970) examined what she termed the ecological organization of intestinal helminth groupings in Clethrionomys gareolus. A number of studies have focussed specifically on the parasites of Microtus pennsylvanicus. Of these, Rausch and Tiner (1949), Erickson (1938), and Kirner et al. (1958) provide the most comprehensive review of parasitism in this species. Notably absent from these reviews are reports of the blood fluke, Schistosomatium douthitti. This worm, the adults of which inhabit the mesenteric veins of their hosts, appears to be primarily a parasite of microtine rodents. Adult worms have been recovered from the mesenteric veins of the muskrat, Ondatra zibethicus (Penner, 1938), the



redbacked vole, <u>Clethrionomys rutilus</u> (Swartz, 1966) and the meadow vole, <u>Microtus pennsylvanicus</u> (Price, 1931). Incidental occurrence has also been reported in the porcupine, <u>Erethizon dorsatum</u> (Choquette <u>et al.</u>, 1973), the meadow jumping mouse, <u>Zapus hudsonius</u> (Whitaker, 1963) and the white-footed mouse, <u>Peromyscus leucopus</u> (Zajac, 1978).

Little work has appeared in the literature concerning the effects of parasitism upon the reproductive output of the host. Wiger (1977) reviewed the literature on the impact of <u>Trypanasoma</u> sp. upon reproduction in their experimental hosts. Weatherly (1971) examined the effects on litter size and litter survival in mice infected with <u>Trichinella spiralis</u> during gestation. More recently, Timm and Cook (1979) analyzed the effect of botfly larvae on reproduction in the white-footed mouse. The authors present a hypothesis in which they consider this host-parasite relationship to be stable and coevolved.



THE STUDY AREA

The composition of a parasite fauna contained within a host species is strongly influenced by the surrounding environment. In view of this, a brief description will be presented of some of the major features of the study area at the Rose Lake Wildlife Research Area in Bath Township, Michigan (sections 22 and 23, T5N, R1W, Clinton County). Each of four trapping grids contained populations of small rodents consisting primarily of the meadow vole (Microtus pennsylvanicus), the meadow jumping mouse (Zapus hudsonius), the white-footed mouse (Peromyscus leucopus), and the deer mouse (P. maniculatus). Populations of these species were examined using a mark and recapture live trapping program. Two of the grids (II and III) were located on moist pond-edge sites while the other two grids (I and IV) were located in dry upland fields. Each set of grids was chosen for its habitat similarities.

The dominant plant species on all four grids was brome grass (<u>Bromus</u> sp.). In contrast with areas of mixed vegetation, there was little litter accumulation beneath even dense stands of this grass. Peak growth with flowering of brome grass in early July was followed by seed



head formation correlated with an overall decrease in precipitation in late July and early August; new growth was noted again in late August and early September.

The two upland grids were quite uniform in composition, consisting almost entirely of brome grass. Occasional patches of goldenrod (<u>Solidago</u> sp.) and Soapwort (<u>Saponaria officinalis</u>) grew on both grids and at least one side of each grid bordered woody vegetation, a deciduous woodland in the case of Grid IV and a hedgerow in the case of Grid I.

Vegetation on the two mesic grids was far more heterogenous. Both bordered on ponds, the edges of which supported dense vegetation, chiefly cattails (<u>Typha</u> sp.) interspersed with lesser amounts of goldenrod and reed canary grass (<u>Phalaris aruidinacea</u>) on Grid II, and a dominant sedge (<u>Carex</u> sp.) plus reed canary grass, goldenrod and joe-pye weed (<u>Eupatorium purpureum</u>) on Grid III. On both grids, the secondary plant species increased in density just beyond the cattail and sedge border, respectively, and then sharply declined in numbers about ten meters from the water's edge. From this point on, both grids extended up a gentle slope covered with brome grass. Dense stands of dogwoods (<u>Cornus</u> sp.), willows (<u>Salix</u> sp.) and multiflora rose (<u>Rosa multiflora</u>) at the edges of these grids dictated an irregular trap arrangement.



Although active growth of vegetation ceased over much of the well-drained habitat dominated by brome grass during mid-summer, vegetation remained lush along the pond borders. It should be noted that when Grids II and III were originally surveyed on June 11, the first row of traps was placed within 1.5 meters of the water's edge. One month earlier, the area covered by the first row of traps had been completely inundated with water. Following the high water conditions, the water level gradually receded with the pond adjoining Grid II drying up completely in early August. The pond bed remained moist, however, and supported lush growth of vegetation for the rest of the season.

A wide range of vertebrates and invertebrates was found on or near the four grid sites. These organisms may play an important role in parasite transmission and a few of the major ones will be mentioned.

In general, predatory species were infrequently observed on all grids. Garter snakes (<u>Thamnophis sirtalis</u>) were the most common, being regularly found on all grids. Two avian predators, the red-tailed hawk (<u>Buteo</u> <u>jamaicensis</u>) and the American kestrel (<u>Falco spaverius</u>), were observed over all the grids at least once during the study. A great-horned owl (<u>Bubo virginiana</u>) was seen twice in trees adjoining Grid III. Weasels (probably <u>Mustela</u> <u>frenata</u>) were caught occasionally in dense vegetation on

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both pond-edge grids. Domestic cats (<u>Felis catus</u>) were observed twice on Grid I. Although never seen, the presence of raccoons (<u>Procyon lotor</u>) was evidenced on all grids by their droppings.

An insectivore, the short-tailed shrew (<u>Blarina</u> <u>brevicauda</u>) was frequently captured on all four grids. The masked shrew (<u>Sorex cinerceus</u>) was never captured during this study, perhaps due to a lack of sensitivity in the trip mechanism of the traps used. Its presence has been shown locally by means of catches in pit-fall traps by Jacquelyn Shier (personal communication, 1979). Other mammals observed on the study sites included white-tailed deer (<u>Odocoileus virginianus</u>) on Grid I and the eastern chipmunk (<u>Tamias striatus</u>) which was occasionally captured on Grid II. One Norway rat (<u>Rattus norvegicus</u>) was captured once on each of Grids I and IV.

Nesting bird species included Henslow's sparrows (<u>Ammodramus henslowii</u>) on Grid I and red-winged blackbirds (<u>Agelaius phoeniceus</u>) on Grids II and III. Eastern meadowlarks (<u>Sturnella magna</u>) and song sparrows (<u>Melospiza</u> <u>melodia</u>) were frequently observed on all four grids. McWhirter and Beaver (1977) give a thorough listing of the avian species reported from this area.

Prominent among the local insect fauna were crickets (Gryllidae) and grasshoppers (<u>Acridadae</u> and <u>Tettigoniidae</u>).



These insects and ants were commonly attracted to the bait in the traps.

The molluscan fauna of these sites is of particular interest when examining the ecology of local parasites which may live in these organisms during part of their life cycles. Land snails and slugs were common on all four grids. <u>Anguispira alternata</u> was common while species of the genera <u>Mesodon</u> and <u>Mexomphyx</u> were less so. Ponds adjoining Grids II and III contained large populations of the pulmonate snails, <u>Lymnea elodes</u> (note: See Clark, 1973, for synonymy and taxonomic status of this species) and <u>Helisoma trivolvis</u>. Other snails collected were <u>Gyraulus parvus</u>, <u>Physa gyrina</u>, <u>Promenetus</u> sp. and members of the amphibious genus Succinea.



MATERIALS AND METHODS

Demographic data on four populations of <u>Microtus</u> <u>pennsylvanicus</u> and several other small rodents were collected on the four study sites between 20 June and 19 September 1978. This was accomplished using a livetrapping, mark and recapture program which employed galvanized sheet metal live-traps produced by L. M. Leathers and Sons, Athens, GA. These traps are 2.5" wide, 3.5" high and 11" long and have a swinging back door which allows for inspection. In each location, a permanent grid of eightmeter spacing consisting of 100 live traps was established. The exact arrangement of traps varied according to the pond edges and shrubby borders in an attempt to cover a maximum amount of grassy area suitable for meadow voles. A pilot trapping study determined which areas were in fact inhabited by M. pennsylvanicus.

Trapping was conducted in seven periods separated by seven-day intervals. Within a period, live traps at each station on a grid were set on four consecutive evenings. Traps were baited in the early evening with a mixture of peanut butter and rolled oats, inspected for captured animals and closed the following morning, and then baited



and reset that evening. Trapping was not conducted during the day to avoid trap mortality due to exposure. Grids I and II were trapped consecutively for four nights followed directly by four nights of trapping on Grids III and IV.

Upon first capture, individual animals were marked for subsequent identification by toe clipping. The following data were recorded for each new animal captured: Species. location on the grid, toe-clip number, sex, weight and reproductive condition. Weights were obtained to the nearest gram using a Pesola spring scale (100 g capacity). Voles were assigned to age classes on the basis of weight (Krebs, et al., 1969) and reproductive condition was assessed using the methods of Keller and Krebs (1970). Male testical position was recorded as scrotal or abdominal. The female reproductive status was judged by the condition of the nipples (either non-visible, visible or lactating), the vaginal orifice (either perforate or nonperforate) and the degree of closure of the pubic symphysis (either closed, slightly open or open). Females with obviously bulging abdomens were considered to be pregnant. The relative value of these different indicators of female reproductive condition will be discussed under Results.

Upon first capture within a trapping period, a complete set of data was recorded for each animal. If the animal was recaptured within the same four-night trapping



period, only the toe-clip number and location of capture on the grid were recorded.

Two assumptions are inherent in this trapping method. First, it is assumed that trapability is random, so that the results are expected to give a representative view of the populations under examination. Second, the assumption is made that any mortality resulting from the trapping experience and marking by use of the toe-clip method is not related to either sex or age of the meadow vole.

During the final trapping period, all Microtus, Zapus and Peromyscus spp. captured were removed alive from the grids. The animals were then maintained for a maximum of four days in the colony room of the MSU Museum. Internal examinations of reproductive condition and parasite fauna were conducted in the laboratory of Dr. Jeffrey F. Williams at the MSU Veterinary Clinical Center. To determine the presence of internal parasites, the voles and mice were first given an intraperitoneal inoculation of a solution containing a lethal dose of sodium pentabarbitol and approximately 100 units of ammonium heparin which was used to prevent the blood from clotting. The immobilized animals were sexed, weighed, measured and external reproductive indicators were recorded. Also at this time, a small amount of blood was withdrawn from a suborbital puncture using a heparinized capillary tube. The blood was used to



prepare smears to check for blood protozoa and to obtain packed-cell volumes.

Examination of the portal and mesenteric venous systems for the presence of <u>Schistosomatium douthitti</u> was carried out via perfusion using a solution of phosphatebuffered saline. To accomplish this, the hepatic portal vein was severed close to the liver, and the buffered saline solution was introduced through the dorsal aorta. The perfusate flowing from the liver and the severed hepatic portal vein was collected and filtered following the method of Zajac (1978). The blood flukes thus collected were sexed and counted under a light microscope.

The gut was next removed and examined for the presence of metazoan parasites. Appropriate sections of the digestive system were slit longitudinally and the contents were washed and decanted in cold water. Helminths were located and counted under a light microscope and preserved in ten per cent buffered neutral formalin for later identification.

The following internal organs were removed, weighed and preserved in formalin: liver, spleen, kidneys, gonads and adrenals.

The cranium of each <u>Microtus</u> was removed and the brain surface was examined under a dissecting microscope for visible cysts of the toxoplasma-like protozoan, <u>Frenkelia</u> microti. The brains were then removed and preserved in



buffered-neutral formalin for later processing and mounting as six-micron sections. These sections were stained using a periodic acid-Schiff stain with a light green counter stain and examined with a light microscope for F. microti.



RESULTS

The results will be presented in two sections, the first one dealing with the demographic characteristics of the four vole populations and the second covering the data obtained from the parasitological examinations. Analyses of the movements of marked voles in relation to their parasite fauna will also be included in the second section. This consideration will be restricted to data obtained on the meadow vole, and information concerning any of the other rodent species captured (<u>Zapus hudsonius</u>, <u>Peromyscus</u> spp. and <u>Mus musculus</u>) will be presented only where appropriate. It should be noted that no evidence of exchange of animals between grids was ever obtained from the recapture of marked individuals.

Vole Populations

A total of 2800 trap-nights per grid were logged resulting in 851 captures of 108 marked voles. Table 1 presents a listing of the numbers of marked individuals on each grid as well as the total number of captures per grid of each sex. In addition, 68 <u>Z</u>. <u>hudsonius</u>, 55 <u>Peromyscus</u> spp. and one Mus musculus were also marked.



TABLE 1

	Grid I		Grid II		Grid III		Grid IV	
	Male	Female	Male	Female	Male	Female	Male	Female
Number of captures	150	92	119	74	174	133	38	13
Number of marked voles	22	15	16	14	24	22	9	5

TOTAL NUMBER OF CAPTURES OF MARKED ANIMALS ON EACH GRID, INCLUDING RECAPTURES

Numbers

The number of voles alive on each grid throughout the study was calculated using the direct enumeration technique described by Krebs (1966). In using this method, the minimum number of animals alive at time t is obtained by summing two figures: (1) the number of animals caught at time t; and (2) the number of previously marked animals caught after time t, but not at that time. Figure 1 graphs the minimum number of voles alive on each of the four grids during the study period. Numbers of animals range from a low of one individual on Grid IV during the final trapping period, to a high of 28 animals on Grid I during the sixth trapping period.

Similar trends include an initial increase in numbers on all grids except Grid IV, and an overall decline in numbers on all four grids during the final trapping period.









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Dynamics of the two water-edge populations (Grid II and III) were similar: the number of animals on both grids first increased, peaked in mid-summer and then declined gradually during the final trapping periods. In contrast, the growth of the two upland populations differed greatly, both from one another and from the two water-edge populations. The minimum number of voles alive on Grid IV declined steadily during the study, reaching a low point of one individual during the final trapping period. In direct contrast with this, the number of marked animals on Grid I increased steadily reaching a high point of 28 animals during trapping period six, then decreasing slightly during the final trapping period. Weight class and reproductive data imply that this increase may not be due to resident breeding but rather to an enlargement of the subadult weight class, perhaps due to emigration (Table 2). This point will be considered further in the next section.

During the final trapping period, all marked voles captured were removed and held alive until parasitological examinations could be performed. This totalled 45 animals, numbering 17, 10, 17 and one animal removed on Grids I-IV, respectively. Table 3 presents a listing of the marked animals according to grid, sex and weight-defined age class.



		Juvenile		Sub	adult	Adult	
		Male	Female	Male	Female	Male	Female
Grid	I	15	16	44	33	14	5
Grid	II	2	1	23	21	27	14
Grid	III	6	16	42	31	24	12
Grid	IV	0	5	23	3	2	0

TABLE 2								
DISTRI	BUTION TO WEI	OF CA	PTURES	ON AGE	EACH CLAS	GRID SS ANI	ACCORD	ING
	SUMME	ED ACR	OSS TH	E SI	UDY H	PERIOI)	

TABLE 3

NUMBER OF MARKED VOLES REMOVED DURING THE FINAL TRAPPING PERIOD

		Juvenile		Sub	adult	Adult		
		Male	Female	Male	Female	Male	Female	Total
Grid	I	0	0	6	6	4	1	17
Grid	II	0	0	2	1	4	3	10
Grid	III	0	0	1	2	8	6	17
Grid	IV	0	0	0	0	1	0	1



Reproduction

Reproductive intensity was evaluated on the basis of a number of external indicators. The use of external characteristics has its limitations, but Krebs <u>et al</u>. (1969) feel that these indicators do provide a crude measure of reproductive output. Using their method, data for each external characteristic have been summed across the whole study period for the purpose of analysis (Table 4). Data on litter size obtained from autopsies will also be presented. Comparisons of reproductive intensity have been limited to Grids I-III; upland Grid IV has been eliminated because the low number of captures and the overall decline in the number of voles on that grid make any comparison of questionable value.

TABLE 4

	Grid I	Grid II	Grid III
Percentage of males possessing scrotal testes	34.2	44.1	45.8
Percentage of females possessing perforate vaginal openings	30.8	36.8	34.9
Percentage of females possessing enlarged nipples	24.0	30.9	23.6

REPRODUCTIVE CHARACTERISTICS OF ANIMALS CAPTURED ON EACH GRID SUMMED ACROSS ALL TRAPPING PERIODS



Male Reproductive Condition

Male voles with scrotal testes were considered to be in breeding condition. This appeared to be a reasonable assumption since upon autopsy all males with scrotal testes possessed clearly visible tubules in the caudal epididymus. a condition indicative of active sperm production (Jameson, 1950). Figure 2 shows the proportion of males with testes in the scrotal position throughout the study on each of the three grids. The reproductive condition of males on the two water-edge grids followed a similar pattern, with a high proportion of males possessing scrotal testes throughout the season. A consistently lower proportion of males were in breeding condition at any one time on upland Grid I. For each grid. captures of males possessing scrotal testes were totalled, and comparisons of the three grids were performed using a Chi-square test corrected for continuity. This test revealed no statistically significant difference between the number of scrotal males on the two water-edge grids $(x^2 = 1.02, 1 \text{ df}, P > .3)$. In contrast, a separate comparison of upland Grid I to each of the two water-edge grids yielded significant values of χ^2 (Grids I and II, $x^2 = 10.56$, 1 df, P < .01; Grids I and III, $x^2 = 17.09$, 1 df, P < .001). Thus, the number of reproductively-active male voles was significantly greater in the wet than in the dryer habitat.











Female Reproductive Condition

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Several external sexual characteristics were used to evaluate female reproductive condition. Because of the extreme subjectivity involved, data concerning the degree of closure of the pubic symphysis was not analyzed. The most easily assessed external sexual characteristic is the condition of the vaginal opening, although this may not be the most reliable indicator of reproduction. Krebs <u>et al</u>. (1969) feel that the best measure of a population's breeding activity is the percentage of females with enlarged nipples, indicative of lactation. In this study, the data obtained on the enlargement of the nipples may not be entirely accurate due to the subjectivity involved and caution should be exercised in the interpretation of these results.

Figures 3 and 4 graph the proportion of female voles possessing perforate vaginal openings and enlarged nipples, respectively. These animals were captured on the three grids throughout the study. Separate comparisons of the numbers of females with perforate vaginal openings and enlarged nipples were made between the three grids and were evaluated using a Chi-square test corrected for continuity. No statistically significant results were obtained from any of the paired comparisons of grids for either characteristic. Figure 3 shows that the occurrence of females with perforate vaginal openings was similar on the two water-edge grids throughout the season. Grid I differed in that the


















majority of females with perforate vaginal openings was concentrated in trapping periods four and five. It should be noted that neither did this increase coincide with nor was it followed by an increase in observed pregnancies.

The frequencies of observed pregnancies varied greatly between the two habitat types. Throughout the course of the study, only two females with obviously bulging abdomens, indicative of pregnancy, were captured on each of the two upland grids. Pregnant females were encountered much more frequently on the two water-edge grids, with ten observed on Grid II and eleven on Grid III.

Further information on reproduction was obtained in the form of embryo counts taken from pregnant females which were autopsied upon final removal. Table 5 lists the numbers of embryos removed from the five pregnant females each examined from Grids I and II, and the six females from Grid III. The failure to find a difference between wet and dry habitats in this and the other analyses of female reproductive condition may be due to the relatively small sample size.

Parasites

Upon removal, all <u>Microtus</u> <u>pennsylvanicus</u> were examined for the presence of helminthic endoparasites. Table 6 summarizes the results and includes information on two protozoan species. Grid IV has been eliminated from the following statistical considerations since only one animal was removed and examined.



Grid II	Grid III
n = 5	n = 6
7	6
7	6
6	6
6	6
5	6
-	5
$\bar{x} = 6.2$	x = 5.8
	Grid II n = 5 7 7 6 6 6 5 - 7 x = 6.2

TABLE 5								
NUMBER	OF PRI	EMBRY	os vo	REMO	VED	FROM AUTO	INDIVIDU OPSY	AL

Parasite Species

As might be expected from knowledge of their life cycles, trematode infections were entirely restricted to voles from the two water-edge grids. Most frequently encountered was the cecal fluke, <u>Quinqueserialis</u> <u>quinqueserialis</u>, with 44.4 percent on the animals from Grid II and 47.1 percent from Grid III harboring infections. Worm burdens ranged from one to 13 individuals with a mean number of three worms. The second most frequently encountered trematode was the blood fluke, <u>Schistosomatium</u> douthitti, which occurred at infection levels of about 11



TABLE 6

NUMBER OF VOLES PARASITIZED (AND PERCENTAGES) ACCORDING TO INDIVIDUAL SPECIES AND GRID

	G	rid I	C	rid II	5	iid III	0	rid IV
	F	= 15		6 = u	-	1 = 17		n = 1
Schistosomatium douthitti		:	г	(11.1)	2	(11.8)	1	:
Quinqueserialis quinqueserialis	i.	1	4	(4.4)	80	(47.1)	ı	ł
Unidentified Trematode		1	,	1	Ч	(6.9)	ı.	ł
Syphacea obvelata	4	(26.7)	e	(33.3)	З	(17.6)	г	(100.0)
Trichuris sp.	1	(6.7)	,	1	2	(29.4)	1	ł
Hymenolepis sp.	ч	(6.7)	ı.	ł	,	1	ı.	1
Anoplocephalid tapeworm l	Ч	(6.7)	ı.	ł	Ч	(6.9)	1	1
Anoplocephalid tapeworm 2		ł	٦	(11.1)	3	(11.8)	1	ł
Frenkelia microti	г	(6.7)	1	ł	ı.	ł	T.	ł
Trypanasoma sp.	1	(6.7)	1	ł	2	(11.8)	۰.	1

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Service Strike



percent on each of the two water-edge grids. Infection levels of this parasite were quite low relative to data from past years in the same general area (Zajac, 1978). In addition, one unidentified trematode was collected from the intestine of a single vole.

The occurrence of infections involving nematodes and cestodes did not appear to be related to the presence or absence of water. The pinworm, Syphacea obvelata, was ubiquitous in its distribution, being found on all four grids (the one animal examined from Grid IV contained an infection of five pinworms). One whipworm, Trichuris sp., was recovered from an animal inhabiting upland Grid I, while five animals from Grid III harbored single infections of this nematode. Adult cestodes were infrequently encountered in the intestines of voles from all three grids and infection levels ranged from 11.1 to 13.3 percent. Two anoplocephalid and one hymenolepid species of tapeworm appear to be represented and in all but one case, single species infections occurred. Three out of the five infections were composed of a single tapeworm. The two exceptions were an individual vole which contained 13 scoleces of a small hymenolepid tapeworm (Hymenolepis sp.) and a vole which contained a single adult of each of the two other species of anoplocephalid tapeworms.

It should be noted that although complete data were not recorded, small (2-3 mm) cysts were occasionally observed in the livers of voles removed from the three grids. These



may be larvae of cestodes belonging to the genus <u>Cladotaenia</u> (Rausch and Tiner, 1949), the adults of which are found in the harrier (<u>Circus cyaneus</u>). This avian predator inhabits the Rose Lake Area (McWhirter and Beaver, 1977) but was not observed during this study. No large cysts indicative of infection with Taenia spp. were observed.

Data were also collected on two protozoan species. Examination of blood-smears reveals infections of a trypanasome (<u>Trypanasoma</u> sp.); however, the prevalence was low (7.3 percent) when compared with that obtained by Dunaway <u>et al</u>. (1968) from <u>Microtus ochrogaster</u> collected in Tennessee. An extremely low prevalence (8.4 percent overall) of the toxoplasma-like protozoan, <u>Frenkelia microti</u> was revealed as a result of the examination of brain tissue. The one infected individual was heavily parasitized and the cyst stage of this protozoan was grossly visible on the surface of the brain. Histological examination of brain sections revealed no further occurrence of this parasite.

Although the four study sites were located within a 1.5 square mile area, no evidence of exchange of individuals between grids was ever observed on the basis of toe-clip and recapture data. Also water-borne infections of trematodes were never found in voles from the upland study site, indicating little or no exchange of individuals from wet areas. In contrast with this, examinations of <u>Zapus</u> hudsonius collected from upland Grid IV revealed that two



out of 14 animals were infected with <u>Schistosomatium</u> <u>douthitti</u>. Patterns of movement of <u>Z</u>. <u>hudsonius</u> appear to be quite different from those of the meadow vole and this point will be discussed in more detail.

Statistical Tests

A comparison of the numbers of animals parasitized with helminth infections from the three grids (Table 7) was performed using the Fisher exact probability test. For the

TABLE 7

NUMBERS (AND PERCENTAGES) OF PARASITIZED AND NONPARASITIZED VOLES ON EACH GRID

		Parasitized	Unparasitized
			onpurubicibeu
Grid I	n = 15	7 (46.6)	8 (53.3)
Grid II	n = 9	8 (88.9)	1 (11.1)
Grid III	n = 17	13 (76.5)	4 (23.5)

purpose of this analysis, each animal was classed as being "parasitized" if it contained an infection of at least one parasitic helminth, or "unparasitized" if no helminths were found upon autopsy. The null hypothesis of no difference in the number of infected animals was examined. A paired comparison of the two water-edge grids indicated that no statistically significant difference existed between the occurrence of parasitized voles (P = .42). On the basis of this test, data from the two water-edge grids were pooled



and compared with the data from upland Grid I. A significant value (P = .024) resulted in the rejection of the null hypothesis of no difference in the number of parasitized animals.

The relationship between the center of activity of a given vole and the nature of its parasitic fauna was examined statistically. The movements of voles on the two water-edge grids were compared relative to the presence or absence of Q. guingueserialis and/or S. douthitti. In order to acquire either of these parasites, an animal must at some time forage at the water's edge, or actually enter it. The eight-meter spacing between the individual traps allowed the distance of capture from the water's edge to be roughly calculated. Capture sites and frequencies of capture were mapped for each vole removed from the water-edge grids. Figures 5 and 6 illustrate maps of representative individuals, four each from Grids II and III. The water's edge lies along the right border of each map. It was noted that individuals containing trematode infections were captured predominantly close to the water's edge (Figure 5, a-c and Figure 6, a-c). From these maps, the average distance away from the water's edge at which each animal was captured was calculated (Table 8). Voles were classed as "parasitized" if they contained trematode infections and as "unparasitized" in their absence. A Mann-Whitney U test was used to examine the one-tailed alternative hypothesis stating that the





- Figure 5. Grid II: Capture sites and frequencies of capture of four representative meadow voles. The water's edge lies along the right border of each map. Below, sex, total number of captures and parasites found upon autopsy are given for each animal.
 - (a) Female: 7 captures 2 Schistosomatium 1 Quinqueserialis quinqueserialis
 - (b) Male: 15 captures 2 Q. quinqueserialis
 - (c) Female: 6 captures
 1 Q. quinqueserialis
 - (d) Female: 13 captures no parasites found

39



1×_4×

с

1.32 minutes









- Figure 6. Grid III: Capture sites and frequencies of capture of four representative meadow voles. The water's edge lies along the right border of each map. Below, sex, total number of captures and parasites found upon autopsy are given for each animal.

 - (b) Male: 17 captures 1 Schistosomatium douthitti 1 Q. quinqueserialis
 - (c) Male: 8 captures
 - 2 <u>S</u>. douthitti
 - 1 Q. quinqueserialis
 - (d) Male: 7 captures no parasites found





Parasitized		Unparasitized
	Grid II	
27.7		53.6
13.7		40.0
2.7		33.8
1.1		20.7
		8.0
x = 11.3		x = 31.2
	Grid III	
39.5		73.6
34.2		66.7
23.3		59.7
23.2		58.3
17.8		43.7
8.5		42.4
8.0		24.7
0.0		10.1
		6.0
x = 19.3		$\bar{x} = 42.8$

TABLE 8 AVERAGE DISTANCE OF CAPTURE IN METERS FROM THE WATER'S EDGE OF "PARASITIZED" AND "UNPARASITIZED" VOLES



mean capture distance away from water is greater for unparasitized animals than for parasitized animals. On each grid, a statistically significant difference resulted in the rejection of the null hypothesis of no differences (Grid II, U = 3, P < .056; Grid III, U = 14, P < .025). It appears therefore that there is a correlation between the location of the center of activity of an individual as indicated by its average distance of capture from the water's edge and the composition of its parasite fauna.

In addition, information was desired on the distance of closest approach to water by each animal as indicated by capture location on the grid. This was considered to be important because even if the majority of captures occur far from water, a single contact with water may be sufficient to cause infection. In order to examine the relationship between closest approach to water and the composition of an animal's parasitic fauna, animals captured at least once in the two rows of traps closest to the water on each grid (a distance of approximately eight meters from the water's edge) were scored as "positive" while those never captured in these rows were scored as "negative." The parasite categories from the previous experiment were retained and a Fisher exact probability test was performed to examine the alternative hypothesis that animals captured at least once close to the water's edge had a greater probability of being infected with trematodes than



those animals not captured in the first two rows of traps. A significant difference resulted in the acceptance of the alternative hypothesis (1 df, P = .03).


DISCUSSION

Distribution of Parasites

The results of the parasitological examinations showed that the habitat in which a vole lived strongly influenced the composition of its parasitic fauna. Trematode infections were entirely restricted to voles from the two water edge sites and consisted mainly of Quinqueserialis quinqueserialis and Schistosomatium douthitti. The intermediate hosts of these two species, the snails Gyraulus parvus and Lymnea elodes, respectively, were found in abundance in the ponds adjoining these sites. Infection levels, as mentioned earlier, were low relative to previous year's data from the same area. This may be due to the series of dry summers which preceded and included this study, during which the ponds dried up in late summer and transmission cycles were most likely interrupted. This, coupled with the relatively short life spans of voles under natural conditions (Hamilton, 1941), could contribute to the low levels of infection observed.

No distinct relationship to habitat type was noted in the occurrence of nematode and cestode infections. The pinworm, Syphacia obvelata, was the most frequently



encountered parasite during this study and its distribution appeared to be random. This parasite possesses a direct life cycle in which frequent contact with other small mammals, rather than the presence of a specialized intermediate host, would be required for the completion of the life cycle. These results are consistent with those of Rausch and Tiner (1949) who noted no difference in the occurrence of this parasite in voles collected in dry and more mesic habitats. In contrast, Mollhagen (1978) observed the highest incidence of Syphacia sigmodontis from Sigmodon hispidus to occur in mesic habitats. One reason for this may be that the viability of the free living stages of this parasite may have been negatively influenced by the aridity of the xeric habitat sampled in much of this study. The occurrence of the three species of cestodes was sporadic and appeared to follow no distinct pattern, although the relatively small number of infections observed may have contributed to this conclusion.

Bush <u>et al</u>. (1978) stated that "one current view of community ecology is that similar habitats are occupied by an essentially constant primary community of species adapted to those habitats and a more variable secondary community. The former provides a basis for similarity, the latter for diversity." A population of definitive hosts is considered to be the equivalent of a community of trophically-similar organisms. Using this framework, a



population of voles may be infected with a primary community of parasites which occur in a variety of habitats over a wide geographical area. This primary community is represented in this study by <u>Syphacia obveleta</u> and may also include one or more of the species of cestodes. The wide distribution of these species is noted in the studies of Erickson (1938) and Rausch and Tiner (1949) and an examination of these works indicates that cestodes of the genus <u>Andrya</u> and <u>Taenia</u> as well as certain nematodes may be included in this community.

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Superimposed upon this community is a secondary community of parasites whose components are derived from a certain environmental habitat within the overall geographical distribution. In this case, a secondary community of parasites whose components are of fresh water origin may be seen in the form of the trematode species whose distribution is restricted to voles inhabiting pond edges. Bush, Holmes and Humphrey (personal communication, 1979) also discussed the presence of a tertiary community of parasites, the occurrence of which is restricted to a specific region within the overall habitat. This may be related to microclimatic site variation which may affect the parasites directly or influence the distribution of various intermediate host species. This tertiary community of parasites is not clearly represented in this study. A larger sample size may be needed to reveal this community, if present.



The low incidence of protozoan infections observed in this study does not allow for a detailed analysis of their distribution. The presence of the toxoplasma-like protozoan, Frenkelia microti in M. pennsylvanicus appears to be the second record for this species (Kirmse, 1965). Dubey (1977), in a recent review, noted that a high incidence of this parasite has been reported to occur in a number of microtine species, but few authors reported the presence of debilitating clinical symptoms. The occurrence of F. microti in only one of the 42 animals examined is curious in that an extensive portion of the brain was involved and cysts were grossly visible on its surface. Histological examinations of all other specimens revealed no further infection. In this case involving such a massive infection, the behavior of the one parasitized animal is of interest. This vole, an adult male, was captured a total of nine times from 25 July to 16 September 1978 and was in reproductive condition during that whole period. No aberrant behavior was noted at the time of removal. These observations serve only to increase our interest in the effects of this poorly-known protozoan upon microtine biology.

In contrast with data obtained from <u>M</u>. <u>pennsylvanicus</u>, two of the 14 specimens of <u>Zapus hudsonius</u> examined from the upland grid sites contained infections of the waterborne trematode, <u>S</u>. <u>douthitti</u>. This was surprising since



these two animals were captured on upland Grid IV, over 40 meters from the nearest free standing water. This is consistent with the observation that movements of the meadow jumping mouse are more extensive than those of the meadow vole. The home ranges of meadow jumping mice are generally larger than those of the meadow vole (Quimby, 1951; Hamilton, 1937). Townsend (1935) suggested that meadow jumping mice tend to wander, and felt that the observed movement was a result of the animals seeking moist areas during the dry part of the summer. Quimby (1951) suggested that the movement is due to a relatively unstable home range, the shape of which is determined by the terrain. Patterns of movement and thus home range size of the meadow jumping mouse may also be strongly influenced by the dietary habits of this species. In contrast with the herbivorous meadow vole which is continually surrounded by its food supply, the meadow jumping mouse is primarily granivorous, utilizing resources which occur in a patchy distribution both in time and in space. Whatever the proximal cause of this movement may be, this activity appears to place these mice in frequent contact with sources of infection by water borne parasites. Involvement of this host species may play a significant role in the maintenance of S. douthitti within certain habitats.



Behavior of Vole Populations

The behavior of vole populations from two distinct types of habitats was examined in relation to their associated parasitic faunas. With the exception of upland Grid IV, all grids housed active populations of Microtus pennsylvanicus along with populations of other small mammals. Densities of voles on the two water-edge grids followed a similar pattern throughout this study (20 June to 19 September 1978), while those from the two upland sites showed widely disparate fluctuations. Since the upland and lowland populations were more or less continuous, it seems improbable that the observed differences were related to the various phases of microtine cycles (i.e., increase phase, decline, etc.). These differences were most likely related to the local variation of the habitat. Getz (1963) and other authors have noted that the meadow vole appears to have a high moisture requirement and is characteristic of moist grasslands and marshes, although it has been recorded from both wet and dry habitats. In a study of vole populations in Michigan, Getz (1960) found higher densities of voles in marshes when compared with old fields.

Pond edge sites perhaps provide voles with a highly optimal and somewhat predictable or constant habitat. This may be reflected in the similar behavior of the two water edge populations of voles in this study. Some variation in the environmental conditions did exist between these two



grids: Standing water remained in the pond adjoining Grid III while the pond adjoining Grid II dried up by early Nonetheless, the pond bed adjoining Grid II August. remained more moist than the surrounding habitat until autumn rains again filled it. The critical factor influencing vole behavior at these sites may be the constant source of moisture (Getz, 1960) which directly affects plant growth. The presence of actively growing plant material may positively affect reproductive output by voles in these areas in a similar fashion as has been demonstrated by Negus and Berger (1979) to occur in Microtus montanus. It was noted during the present study that plant growth essentially ceased in midsummer on the upland sites which were dominated by brome grass. The effects of the midsummer drying were particularly pronounced on Grid IV and on this grid the vole population declined consistently. Grid I was set up in a grassy depression and on this grid population levels stayed high, although the factors contributing to the observed high density may differ from those in operation on the two water edge grids as already noted.

On a local scale, yearly variation in the levels of precipitation could influence the demography of voles living in dry, marginally suitable habitat. Conversely, highly suitable pond edge habitats may provide voles with a somewhat stable and predictable environment. This stability is perhaps reflected in terms of reproductive output as



maintained through compounds (Negus <u>et al</u>., 1977) found in actively growing plant material. The data show that male reproductive activity is definitely higher on the two water edge grids than on the two upland grids, but female reproductive indicators do not show this trend. The observation that, in comparison with upland Grid I, nearly four times as many pregnancies were noted on Grid II and nearly three times as many on Grid III indicates that the hypothesis of differential reproductive output from wet and dry grids deserves further testing. The failure to find a difference between wet and dry habitats may be due to the relatively small sample size.

We may speculate on the influence of differential reproductive output upon parasitic relationships: In certain dry seasons, the majority of reproduction within a local area may arise from voles inhabiting favorable moist habitats. This hypothesized reproductive effort may have a strong influence upon the fixation within local vole populations of genetically controlled resistance to the high parasitic assault experienced in water edge areas. The local effects of habitat on vole populations will be considered further in the following section concerning parasitic interactions.



Relationship Between the Meadow Vole and its Parasitic Fauna

One intention of this study was to try and gain some information concerning the impact of a naturally-occurring parasite complex upon its host population. In order to examine the influence of parasitic infection, the prevalence of helminth parasitism of meadow voles was compared between the two habitat types. A significantly higher prevalence of parasitism was shown to occur on the water edge grids when compared with the upland site. It has already been noted that reproductive activity appeared to be higher on the two water edge grids than on the upland grids when evaluated on the basis of at least one indicator, and was not significantly reduced. Meadow voles living near water may achieve a higher reproductive output and incur a higher parasite burden relative to voles living in drver upland sites. This is consistent with the assumption that in a coevolved host-parasite system. little or no damage to the host will be incurred by the "prudent parasite." Further aspects of the coevolutionary nature of microtine host-parasite systems will be considered in an upcoming section. It should be stressed that although these data imply that high reproductive output occurs in areas of high parasitic infection, the actual impact of the parasite population upon the host population cannot be clearly defined from this sort of field study. Certain environmental factors appear to enhance reproduction in the vole and it



is possible that this may mask detrimental effects exerted by the parasites. It is also possible that parasitic infection negatively influences juvenile survivorship and that this effect remained undetected in this study. It could be argued that increased reproductive output on water edge grids may result as a response to increased mortality due to parasitism. Detrimental effects which might lead to mortality have not been demonstrated for at least one common parasite of the meadow vole, <u>Schistosomatium douthitti</u>. Laboratory studies are needed to properly address this contention.

The observation that reproduction in meadow voles remained high in areas of frequent parasitism implies two important points: First, that some degree of coordination of life cycles and resistance occurs between the parasite and host populations, and second, that high reproductive potential coupled with a rapid population turnover rate in the face of major parasitic assault might allow for genetic selection of immunological resistance to parasitic damage.

Two final notes of caution in interpreting these results should be mentioned. First, it is unlikely that all parasite species had an equal effect upon the host as was assumed in this analysis. Also, for managability, the effects of arthropod and protozoan parasites were not considered. Second, different results might possibly have



been obtained if this study had been conducted in a year of higher parasitic infection as was seen by Zajac (1978). A controlled experiment which involved artificial infections would give a more accurate view of the impact of naturallyoccurring parasites upon their host species, at least partially freeing the investigator from the confounding influence of environmental effects.

Statistical tests showed an apparent correlation between the location of the center of activity of an individual vole as indicated by average distance of capture from the water's edge and the composition of its parasitic fauna. The average distance of capture from the water's edge of voles infected with water borne trematodes was significantly smaller than that of animals lacking these infections. This indicates that relatively little movement by resident voles occurred away from the site of infection during the threemonth course of this study, although it does not reflect upon the behavior of dispersing animals. This observation is consistent with that of Getz (1961) who found relatively little movement of young voles away from their birth site and noted that many female offspring constructed nests within the home ranges of their mothers. These findings are of particular interest in that they incorporated a temporal as well as spatial element into our knowledge of the distribution of a parasite population within a population of one host species. A clearer definition of the behavior and



movements of infected host individuals aids our understanding of the functioning of naturally-occurring host-parasite systems in that these factors determine the continued maintenance and dispersal of the parasite population.

The final statistical analysis performed involved an examination of the helminth fauna of an animal in relation to its closest approach to the water's edge, as indicated by capture location on the grid. As was stated earlier, this was considered to be important because even if the majority of captures occurred far from the water's edge, a single contact with water may be sufficient to cause infection with a water borne trematode. The results show that voles captured at least once in the first two rows of traps closest to the pond edge had a significantly greater chance of being infected with water borne trematodes than did voles captured elsewhere on the grid. The previous analysis showed that the prevalence of infection with trematodes within the vole populations under study dropped off rapidly as the distance from the water's edge increases (Table 8). This analysis relates the probability of infection by trematodes to the amount of dispersion of a vole's home range as well as the location of that home range.

It appears that certain aspects of the biology of the meadow vole have strongly influenced the nature of the parasitic relationships associated with this species. Rausch and Tiner (1949) attempted to examine the effects of



microtine population fluctuations upon the population densities of associated parasitic species but found no definite connection between population densities of voles and parasite density. They felt that both quantitative and qualitative differences in helminth infections were seasonal or geographic in nature. The present study has demonstrated the effects of local habitat variation upon the composition of the parasitic fauna of the meadow vole. The preference for moist habitat by this species often places these animals in direct contact with a major source of parasitic infection. In relatively constant pond edge habitats, survival of meadow voles appears to be improved (Getz, 1960) and reproductive output may be enhanced. An increase in the already high fecundity of this species coupled with a frequent parasitic assault in what appears to be a highly favorable habitat may contribute to the formation of highly coordinated and somewhat stable host-parasite systems.

<u>Schistosomatium</u> <u>douthitti</u> and <u>Microtus</u> <u>pennsylvanicus</u> as a <u>Host-Parasite</u> System: Synthesis and Speculation

In the final section of this discussion, the relationship between the meadow vole and one of its naturallyoccurring parasites, the blood fluke, <u>Schistosomatium</u> <u>douthitti</u>, will be examined. Studies in the literature combined with data from the present study provide the basis for this consideration. Ecologically-significant parameters



along with selective pressures which have shaped this system will be discussed.

The blood fluke, S. douthitti, is found in the mesenteric veins of its mammalian hosts and appears to be primarily a parasite of microtine rodents. Malek (1977) gives a comprehensive review of the literature available on the biology of this species. As with all schistosomes, infection of the mammalian definitive host occurs by direct penetration of the skin by the cercarial stage. For this to be accomplished, the host must actually enter water containing cercaria. Although it is generally not considered to be a semiaquatic animal, the meadow vole frequently enters the water and inhabits marshes and pond borders (Getz, 1961; Blair, 1939). Activity patterns of the vole appear to be coordinated with the time of cercarial release from the intermediate molluscan host in that maximum cercarial output occurs at dusk (Oliver, 1951) when rodent activity is high (Hamilton, 1957). Cercarial shedding also occurs at this time in the rodent strains of the blood fluke, Schistosoma japonicum (Kennedy, 1975). In contrast, the cercarial shedding of at least one human schistosome, S. mansoni, occurs around mid-day when the chances of human water entry are high.

The coordination of the life cycle of this parasite with that of its host may also be seen in the time of maximum annual shedding of cercaria from infected snails.



Bournes (1961) and Blankespoor (personal communication, 1979) report that shedding of cercaria reaches a peak in mid-summer. High cercarial shedding at this time may be correlated with two aspects of host population biology. First, populations of voles reach an annual high point at this time following the first major reproductive bout in spring and early summer (Figure 1) which would allow for a maximum number of potential host individuals to be exposed to infection. Second, during spring when rainfall is frequent and flooding can be expected, both snails and cercaria would stand the chance of being highly dispersed as a result of variations in water level. By mid-summer, the pond edges have receded and snail populations, and thus cercaria, are concentrated within a relatively small area at the pond border which experiences frequent vole activity. Also it might be speculated that as the overall habitat dries out in mid-summer, densities of the water-limited meadow vole may increase in the thick vegetation along the pond borders relative to the rest of the habitat. Once again, a large number of host individuals would be exposed to a source of infection.

The high levels of infection achieved by <u>S</u>. <u>douthitti</u> in the meadow vole once again indicate that some degree of coordination exists between these two organisms. Zajac (1978) has reported worm burdens ranging from eight to 236 adult parasites recovered from wild-caught voles. Tissue



response to ova produced by these parasites is minimal. Heavily-infected animals appear healthy and Zajac notes that in light of the heavy predation pressure experienced by voles (Burt, 1945), any reduction in an animal's fitness would be expected to result in its removal from the population. The author speculates that the parasite and its associated tissue reaction do not affect the vole's performance adversely. In striking contrast to this, experimental studies have shown that a challenge of only 20 cercaria was sufficient to kill the non-natural host, the house mouse, Mus musculus.

These observations point to a high degree of compatability between the vole and parasite and suggest a long evolutionary association between the two species. Zajac (1978) also noted that subadult and adult voles have higher levels of infection along with heavier worm burdens than do juvenile voles. The presence of large worm burdens only in older animals suggested to her that reinfection may occur during the animal's lifetime. This appears to be in contrast with the situation seen in human infections by schistosomes in which some degree of acquired resistance to reinfection is presumed to occur (Kennedy, 1975).

It seems likely that the short life expectancy of \underline{M} . <u>pennsylvanicus</u> would have some impact upon the maintenance of <u>S</u>. <u>douthitti</u> infections within a given habitat. The average survival time of voles in the field has been



calculated as 2.7 months (Getz, 1960), about 4.2 months (Blair, 1948), and a maximum as much as 16 months (Hamilton, 1941). These low expectancies would still allow enough time for schistosome development and egg production, in that Price (1931) observed egg production approximately 30 days after infection. While other mammalian schistosomes are restricted to tropical and subtropical regions, pronounced seasonality severely limits the time span over which this parasite can be cycled. The impact of seasonal restriction upon the life cycle of S. douthitti combined with the relatively short life expectancy of the meadow vole imply that maintenance of the infection in vole populations throughout the winter is unlikely. In years of high prevalence, some infected voles may survive to continue the cycle the following spring, but in years of environmental stress and thus low infection levels as observed in this study, the infection has a fair chance of declining to extinction in vole populations.

This speculation brings into question the role of other host species in maintaining <u>S</u>. <u>douthitti</u> infections within a given habitat. Malek (1974) found that in certain areas, infections are maintained over the winter in the intermediate molluscan host, <u>Lymnea elodes</u>. Blankespoor (personal communication, 1979) is currently studying other aspects of the role of the molluscan imtermediate host in this cycle.



The other principal mammalian host of S. douthitti, the muskrat, Ondatra zibethicus, is likely to play an important role in cycling this parasite, although the nature of this role is poorly understood. Penner (1942) felt that this species was the most important definitive host of S. douthitti. In contrast with the high infections level of 70 percent from M. pennsylvanicus found by Zajac (1978), Penner (1938) found only 10 percent of the 330 muskrats which he examined to be infected. This prevalence rate seems low and may reflect the author's recovery techniques (Penner, personal communication, 1979). The specimens had been captured by trappers for their pelts, and clotted blood may have made the recovery of worms from the extensive cecal venous system difficult. Penner (personal communication, 1979) also observed the highest prevalence of infection to occur in young muskrats which may imply the presence of acquired resistance or simply reflect behavioral patterns which determine the amount of contact with infective stages.

Although findings in the literature are in no way conclusive, the muskrat may serve as a long distance disperser of <u>S</u>. <u>douthitti</u> infections. The relatively larger territorial requirements of the muskrat result in a more extensive movement by this animal. Shanks and Arthur (1952) reported that muskrats living in pond habitats tended to move from pond to pond, and Errington (1939) reported that during spring and fall periods of movement, muskrats may


travel over land more than 20 miles, presumably in search of more favorable habitat. These movements may serve to inoculate new sites as well as reestablish the infection where local extinctions have occurred.

It is also possible that the muskrat may maintain infections within an area when hypothesized local extinctions occur in populations of <u>M</u>. <u>pennsylvanicus</u>. This is based on the assumption that muskrats are relatively longer lived, although the findings of Mathiak (1966) make this difficult to interpret since he reported an 87 percent mortality in muskrats the first year and a 98 percent removal by the second season. These data may reflect the influence of trapping rather than natural removal, thus confounding any interpretation.

The involvement of the meadow jumping mouse, <u>Zapus</u> <u>hudsonius</u>, as a definitive host of <u>S</u>. <u>douthitti</u> has already been considered to some extent. It is interesting to note that during this study in which the level of <u>S</u>. <u>douthitti</u> prevalence in the meadow vole was low (7 percent overall), a similar prevalence of 10 percent was observed in jumping mice collected from all study sites combined. Carmichael and Muchlinski (in press) demonstrated that <u>S</u>. <u>douthitti</u> survives hibernation in the meadow jumping mouse and egg production by worms was noted in animals which had recently been aroused from hibernation. The meadow jumping mouse may serve as a long-term reservoir of S. douthitti,



maintaining the infection within an area over the winter while in hibernation or when populations of <u>M</u>. <u>pennsylvanicus</u> undergo drastic fluctuations in numbers. Also the relatively longer lived meadow jumping mouse (Quimby, 1951) may maintain infections within an area for a longer time following the disruption of the cycle due to drought and temporary elimination of intermediate host habitat. It should be noted, however, any proposed role of the meadow jumping mouse in maintaining the life cycle of <u>S</u>. <u>douthitti</u> is purely speculative until it has been demonstrated that these mice actually pass the eggs of this fluke.

The previous considerations represent only a very few of the factors which contribute to the successful functioning of a highly coordinated host-parasite system and which convey the complexity and dynamic nature of this interaction. As with most naturally-occurring host-parasite systems, further work is needed both in the laboratory and in the field if we are to understand more fully the maintenance of this unique system.

Summary

The data collected in this study indicate that populations of voles living near water incur a higher parasite burden when compared with local populations of voles inhabiting drier upland sites. Increased moisture along pond edges presumably provides voles with a continual



source of an actively growing food supply which may be favoring increased reproductive output. Population concentrations along the water's edge bring voles in direct contact with a major source of parasitic infections. This may lead to parasite burdens which differ both in composition and intensity from those of other local vole populations. The life cycle of at least one trematode, <u>S</u>. <u>douthitti</u>, appears to be highly coordinated with the activity of <u>M</u>. <u>pennsylvanicus</u>, and these two organisms may represent a coevolved host-parasite system.

The tendency of voles to inhabit moist areas appears to have a strong impact upon this system and a selective regime resulting in resistance to parasitic damage in the vole as well as a high degree of coordination between the population dynamics of both species may be functioning. These selective forces may tend to stabilize the system, but as Kennedy (1975) points out, "Parasite populations are still liable to large fluctuations because of their dependence on climatic factors." He notes that climate influences the prevalance of infection, while host response controls the level of infection within the host, and thus introduces stability.

The findings of this study point toward a number of areas of further research if we are to more fully understand the dynamics of this and other host-parasite systems. A laboratory study would be useful in determining the actual



impact which <u>S</u>. <u>douthitti</u> has upon the meadow vole, and this might be measured in terms of reproductive output and juvenile survivorship. Much work is needed in evaluating the role of other host species in maintaining this cycle. A more precise knowledge of the population processes of the intermediate host species in relation to parasitic infection would aid in any attempt to model the dynamics of this system. Also, the role of the muskrat in this parasitic system deserves further study and reevaluation.

This study may aid in our overall understanding of the functioning of host-parasite systems. The occurrence of S. douthitti in local populations of the meadow vole provides us with a readily available model with which to examine the ecological constraints upon host-parasite systems involving schistosomes. This investigation may have application to studies concerning the ecology of human schistosomiasis, particularly due to the involvement of wild rodents in most schistosome life cycles. Cohen (1977) summarized the need for studies of this sort when he said, "The control or eradication of schistosomiasis is a truly ecological as opposed to a purely medical or technological problem." We are still far from understanding the ecology of the schistosomes, and this group represents one of the most intensively studied families of parasites. Further research is needed on all phases of parasite ecology.



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