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A STUDY OF LOUSE POPULATIONS ON THE  
MEADOW VOLE AND DEER MOUSE

*By*

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## A STUDY OF LOUSE POPULATIONS ON THE MEADOW VOLE AND DEER MOUSE<sup>1</sup>

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### INTRODUCTION

In a recent paper (Cook and Beer 1955) we described the summer louse populations from three species of cricetid rodents from northern Minnesota. Wide year to year differences were recorded in both rate and size of the infestations. In that paper we concluded that these differences could be accounted for by either year to year differences or by annual variations in the sequence of phenological changes. It was felt that the

study of at least one host species and its lice collected over a full year from one locality would help to clarify the problem of the yearly variation in louse populations and provide more adequate data for the analyses and interpretation of these populations.

### *Scope of Study*

The present discussion is based upon a full year's observations on the louse species *Hoplopleura acanthopus* (Burm.) and *H. hesperomydis* (Osb.) infesting the meadow vole (*Microtus pennsylvani-*

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cus Ord) and the deer mouse (*Peromyscus maniculatus bairdii* Hoy and Kennecott) respectively for a full year. The study was designed to indicate whether changes in size of louse populations and rates of infestation that have been noted on small rodents from year to year were due to seasonal or annual variations, and to describe the population from one area over a whole year as accurately as possible.

### The Area

The host specimens were all collected at the Agricultural Experiment Station at Rosemount, located 20 miles south of St. Paul, Minnesota. The region is an old outwash plain with flat to slightly rolling terrain. The soils of the area are composed of about 24 inches of light sandy loam underlain with gravel. They are well drained, and there is no standing water, with the exception of a period during the spring thaw when the soil is still frozen. The Experiment Station is devoted largely to developmental work in diversified agriculture.

The climate is typically continental with much of the precipitation coming in the summer months. During the year of the study there were no meteorological phenomena that diverged appreciably from the normal. There was a continuous snow cover from the last week in November to the last week in March. This snow cover appeared to have little effect on the activities of the meadow voles, but it did affect their availability to our sampling methods. The snow cover appeared to curtail the movements of the deer mice as well as to affect their availability.

The majority of the meadow voles were taken from fields planted to red clover, alfalfa, and oats, or from fence rows and other grassy waste areas adjacent to these cultivated fields. The deer mice were taken largely in open waste areas and in corn, alfalfa, and clover fields. They were not regularly taken in the dense cover of the fence rows.

## THE HOST POPULATION

### Sampling

The host samples were collected at approximately two-week intervals between July 16, 1954 and July 30, 1955. During the snow-free period, trap lines were located so as to sample all available habitats. These lines were composed of 67 trap stations spaced at about 15-foot intervals. Each station was provided with three standard snap traps baited with peanut butter. The lines were left out for three days and the trapped animals were picked up each morning. Since the trapping procedure was standardized, it is possible to use

trap success as an index to host population density. During the winter when a snow cover was present, the traps were set where mouse activity was apparent. The most productive spots were the holes that came up to or near the surface of the snow. Drifting snow often made it necessary to reset the traps every day. Consequently, it was not practical to attempt to standardize the winter trapping methods, and the trapping success ratio cannot be used as an index to population density during this period.

The samples of meadow voles ranged in number from 56 to 132 per month. The total meadow vole sample was 1,004 specimens of which 979 were suitable for use in this study. The samples of deer mice ranged in numbers from 21 to 393 per month. The total number taken was 1,904.

### Host Population Structure

At the period of the first collection in the latter part of July the meadow vole population was at a moderate level as indicated by an index of 25 captures per 1,000 trap station days. The population density index increased to about 45 captures per 1,000 trap station days by the end of October. This was followed by a sharp rise in apparent density as indicated by a success ratio of 86 captures per 1,000 trap station days. Snow fell during the last week in November, and by the first week in December the ground was covered for the winter. Between the first of December and the first of April the trapping success ratio was meaningless, but our general observations indicated that the meadow vole density remained high and possibly increased slightly. During the last few days of March the snow melted rapidly and the meadow voles were seen in considerable numbers wherever there was a little dry ground. This period of thawing apparently caused many animals to migrate. The drop in population at this time as indicated by a trapping success ratio of 6 captures per 1,000 trap station days suggests that a large portion of the population was killed by exposure, predators, and accidents. By the second half of April the remaining meadow voles were concentrated in fence rows and the success ratios here were high although the general population was at a moderately low level. The general density climbed steadily from 6 captures per 1,000 trap station days in early April to about 31 captures per 1,000 trap station days in late July which was approximately the same as when the study started the previous July.

The first collection of deer mice revealed a moderate population density as indicated by the capture of 54 animals per 1,000 trap station days.

TABLE I. Infestation rates and population structures of *H. acanthopus* on the several age classes of male meadow voles

Body length in mm.	Est. age in days	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
							% ♂ ♂	% ♀ ♀	% 3rd	% 2nd	% 1st
60- 89.....	Nestlings	66	43	65	491	11.4	23.6	30.3	1.8	13.0	31.2
90-102.....	16-24	181	112	62	1120	10.0	33.4	36.9	1.8	7.8	20.0
103-111.....	25-33	163	122	75	3281	26.9	25.8	30.6	3.4	8.6	31.5
112-117.....	34-42	62	54	87	1766	32.7	25.9	27.9	10.3	11.5	24.1
118-123.....	43-51	39	37	95	1272	34.3	26.2	21.9	4.1	10.1	37.7
124-126.....	52-60	13	11	85	1249	113.5	21.3	23.4	3.5	9.8	42.0
127+.....	61+	12	11	92	668	60.7	19.9	21.8	4.5	13.6	40.1
		536	390		9847						

TABLE II. Infestation rate and population structures of *H. acanthopus* on the several age classes of the female meadow voles

Body length in mm.	Est. age in days	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
							% ♂ ♂	% ♀ ♀	% 3rd	% 2nd	% 1st
60- 83.....	Nestlings	28	16	59	106	6.6	25.5	28.3	10.4	17.9	17.9
94- 98.....	16-24	120	74	61	869	11.7	32.3	35.0	1.3	8.5	23.0
99-107.....	25-33	119	74	62	465	6.3	39.8	41.9	0.8	4.1	13.3
108-114.....	34-42	68	39	57	328	8.4	38.7	41.5	1.8	7.0	10.9
115-120.....	43-51	54	36	67	289	8.0	43.9	43.2	1.0	2.1	9.7
121-124.....	52-60	24	14	56	456	32.6	22.8	22.3	1.1	3.5	50.2
125+.....	61+	17	9	53	47	5.2	55.3	42.5	2.1	0	0
		430	262		2560						

The density steadily climbed until a success ratio of 221 deer mice were trapped per 1,000 trap station days in the last half of November. After snow covered the ground the trap success ratio immediately became low but restricted activity rather than lowered density is assumed to be responsible. During the first part of April when standardized trapping was resumed, 34 deer mice were trapped per 1,000 trap station days. This increased gradually to 50 animals per 1,000 trap station days by the first week in August; thus, the population density at the end of our sampling year was very like that obtained at the beginning.

Since there were no marked animals of known age to use as guides as to the age of the hosts, it was necessary to fall back on studies from other areas for aging criteria. The grouping of the meadow voles into age classes is based primarily upon the work of Hamilton (1937) and the deer mice on the information published by Svihla (1935). Hamilton's (1937) paper on the meadow vole gives growth curves, expressed in grams, based upon animals of known age. Because the animals in our study were frequently wet when found in the traps and were occasionally attacked by shrews or certain scavenger beetles, it was often impossible to obtain their weights. It was thus

necessary to estimate age on the basis of body length. Body-length-total-weight relationship curves were constructed for both the male and female meadow voles trapped during this study, and the age of each meadow vole was estimated from these. The estimated ages of the several size classes are given in Tables I and II. Recently Barbehenn (1955) has suggested that the rate of gain in weight given by Hamilton (1937) may not be reached in many populations. If this was the case in our meadow vole population the estimated age structures would have to be modified to show a larger proportion of older animals. However, the size at which sexual maturity is reached in the meadow voles we studied agrees very well with Hamilton's (1937) data. While we realize that there are weaknesses in this procedure, we feel that it does give a relative basis for the interpretation of the ectoparasite data.

A very large proportion of the meadow vole population was made up of young animals, with approximately 34% of the females and 40% of the males under 24 days of age. Only 4% of the females and 3% of the males were estimated to be over 60 days of age. Barbehenn's (1955) data suggest that possibly as many as 20% could be over 60 days of age. Even this latter figure shows

TABLE III. Infestation rate and population structure of *H. hesperomydis* on the various size classes of male and female deer mice

Body length in mm.	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
						% ♂♂	% ♀♀	%3rd	%2nd	%1st
60- 42.....	15	3	20.0	4	1.3	25	75	0	0	0
65- 69.....	52	14	26.9	33	2.4	21.2	57.6	3.0	6.0	12.1
70- 74.....	159	47	29.6	356	7.6	20.2	33.7	2.5	9.3	34.3
75- 79.....	372	138	37.1	859	6.2	27.1	44.2	3.3	6.3	19.1
80- 84.....	517	197	38.1	1150	5.8	31.3	42.2	1.6	6.5	18.3
85- 89.....	413	122	29.5	632	5.2	29.1	46.0	1.5	3.5	19.8
90- 94.....	258	85	32.9	315	3.7	35.5	42.2	3.2	5.4	13.7
95- 99.....	83	24	28.9	291	12.1	16.9	24.0	5.8	11.3	41.9
100-105.....	20	5	25.0	25	5.0	36.0	52.0	4.0	0	8.0
	1189	635	33.6%	3665	5.77	29.1%	41.3%	2.6%	6.4%	21.6%

a very heavy proportion of young animals. The rate of population turnover in the meadow vole is very high and it is apparently the unusual individual that even approaches the age of one year. This high population turnover must pose a considerable survival problem for the parasite populations. Since only 3 to possibly 20% of the male meadow voles in the populations sampled were over 60 days of age, the very transient nature of the louse habitat is strikingly apparent.

The meadow voles were reproducing in every month of the year with little indication of variation except during March when but few females were found to be pregnant. Nearly all of the animals were reproductively active by the time they were an estimated 33 days of age. While the reproductive rates appeared to be high throughout the winter, the proportion of meadow voles under an estimated 16 days of age was somewhat lower during this time than in the summer. This might reflect either a reduced rate of survival of nestlings or reduced activity of this group under snow conditions.

There is considerable variation in the age structure of the several samples of meadow voles. It is difficult to interpret these changes but the low proportion of adults in the November sample can be correlated with the sudden increase in host population at that time. The shift from a low proportion of adults during the winter to a high proportion in April can be correlated with the period of stress due to the spring thaw.

The grouping of the deer mice into age classes has been rather arbitrary. According to Svihla (1935) the young deer mice leave the nest when they are approximately 67 mm in body length. Mice smaller than this are here considered to be still attached to the nest and under maternal care and are called nestlings. The transition from juvenile to sub-adult pelage occurs when the mice

are about 75 mm long. There is little or no reproductive activity in the group between 68 and 75 mm, and the group is considered, therefore, to be juvenile. The molt from the sub-adult to adult pelage occurs when the animals are about 85 mm long. Many of the animals between 77 and 85 mm long are reproductively active, and they are considered to be sub-adults. All animals 86 mm long and longer are considered to be adults. A considerable proportion of the population is made up of adult animals suggesting that they are moderately long-lived (Table III). Many probably live for as long as one year, although the life expectancy of a mouse leaving the nest as a juvenile is certainly much less than this.

The deer mice were found to be seasonal breeders. Reproductive activity started about April 1 and ended gradually during October.

#### THE PARASITE POPULATION

##### Methods

The method of handling the host specimens to prevent contamination and loss of lice and of recovering the total louse population has been described by Cook (1954 a and b) and Cook and Beer (1955).

The possibility that the louse population figures are somewhat low due to loss of lice in the traps before the host specimens are picked up has been considered. The anatomy of the lice, with their highly modified legs, makes it unlikely that they would actively leave the host. In the summer it has been noted that some lice crawl to the ends of the hairs after the host dies. While some lice are undoubtedly lost under these conditions, we do not believe that this loss has been great enough to affect appreciably our parasite population figures. During the winter months such loss is much less likely as the lice were observed to remain next to the host's skin until immobilized by the cold. We

TABLE IV. Infestation rate and population structure of *H. acanthopus* on male meadow voles per month

	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
						% ♂ ♂	% ♀ ♀	% 3rd	% 2nd	% 1st
J16-A15.....	31	12	39	123	10.2	20.3	23.6	4.9	5.7	45.5
A16-S16.....	41	17	41	301	17.7	18.9	20.3	2.3	6.8	50.2
S16-O15.....	43	16	37	91	5.6	31.9	41.7	2.2	5.5	18.7
O16-N15.....	57	42	74	1422	33.9	20.9	22.8	2.9	12.9	40.4
N16-D15.....	55	49	89	712	14.5	30.7	34.8	1.4	7.2	25.8
D16-J15.....	41	33	80	455	13.8	29.4	31.9	1.7	10.5	26.4
J16-F14.....	42	33	79	313	9.5	26.5	35.1	2.5	12.1	23.6
F15-M15.....	54	33	61	482	14.6	38.2	43.9	0.8	3.9	13.1
M16-A15.....	28	27	96	1565	60.2	26.2	30.5	3.9	9.3	30.1
A16-M15.....	37	37	100	2408	63.4	23.0	28.3	5.1	10.9	32.6
M16-J15.....	65	57	88	1249	21.9	26.1	25.7	11.5	9.5	27.1
J16-J15.....	27	22	81	256	11.6	27.3	30.5	3.1	9.4	29.7
J16.....	21	16	76	477	29.8	20.3	24.7	5.4	10.9	38.6
	542	394	72.6%	9854	25.1	25.2%	28.9%	4.5%	9.9%	31.4%

have made numerous attempts to find lice on the traps and on the snow around the dead hosts, uniformly without success. When removed from the traps the hosts were promptly placed in individual plastic bags so no further loss could occur. Only a few lice were dislodged from the hosts in the bags in which they were transported and stored. While no actual count was made, probably no more than 200 of the 16,288 lice were recovered from the plastic bags rather than directly from the host skin. If an equal number had fallen from the hosts prior to the time they were removed from the traps, the loss would be no more than 2%. This would slightly depress our summer counts relative to winter counts but should have little effect on the conclusions.

#### Rate of Infestation

Of the 979 meadow voles examined, 660 were found to harbor lice. In total, 12,550 lice were recovered from the infested hosts. All of these lice, except for a single specimen of *Hoplopleura hesperomydis*, which is the louse normally found on members of the genus *Peromyscus*, and a single Trichodectid nymph, which probably came from the pocket gopher (*Geomys bursarius*), were *Hoplopleura acanthopus*. The single specimen of *H. hesperomydis* was found on a female meadow vole taken on February 7, 1955, and the Trichodectid was from a female taken on January 6, 1955.

Of the 1,904 deer mice examined, 641 were infested with a total of 3,738 *Hoplopleura hesperomydis*. Two of the male mice were infested with a single Trichodectid each, but no other species of Anoplura or Mallophaga was found. These data further confirm the high degree of host specificity that generally has been assumed.

#### Rate of Infestation and Seasonal Variation

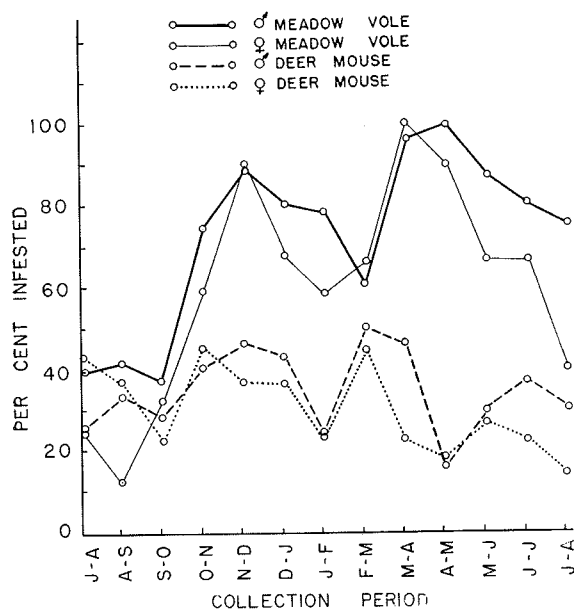
A striking feature observed was the difference in the rate of infestation between the male and female meadow voles (Tables IV and V) in contrast to a lack of any such difference in the deer mice. The combined data show over the whole year that 72.6% of the male meadow voles harbored lice as opposed to only 60.9% of the females. Calculations give a *k* value (Treloar 1941) of 3.92 ( $P = 0.0001$ ) for these data indicating a highly significant difference in rate between male and female hosts. On the other hand the deer mice show little variation between sexes. The combined data show 32.6% of the females and 34.4% of the males infested. The *k* value for this is 0.88 ( $P = 0.378$ ) and it is most likely that no real differences exist.

In addition to differences in infestation rate between sexes in the meadow voles there is evident a month to month difference throughout the year with a peak in infestation rate occurring in the period from the last part of October to the end of December and a high peak occurring from the last half of March to the middle of May (Tables IV and V and Figure 1). An analysis of variance of the rate of infestation each month over the whole year results in an *F* value of 12.05. This indicates that the differences shown from month to month in the infestation rate are highly significant ( $P < .01$ ).

In the deer mice month to month differences in rate of infestation are evident also with peaks in the fall and late winter (Table VI and Figure 1). Analysis of the data for the deer mice for each sex each month over the year yields an *F* value for the monthly variation of 2.87. This is significant to the 5% level. Thus, the deer mouse data show statistically significant differences from

TABLE V. Infestation rate and population structure of *H. acanthopus* on female meadow voles per month

	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
						%♂♂	%♀♀	%3rd	%2nd	%1st
J16-A15.....	29	7	24	17	2.4	52.9	23.5	0	0	23.5
A16-S15.....	34	4	12	9	2.2	55.5	44.5	0	0	0
S16-O15.....	25	8	32	22	2.7	36.4	50.0	4.5	0	9.1
O16-N15.....	47	28	59	160	5.7	39.4	49.4	1.2	2.5	7.5
N16-D15.....	30	27	90	300	11.1	41.3	38.3	1.7	3.7	15.00
D16-J15.....	38	26	68	106	4.1	45.3	40.6	0	7.5	6.6
J16-F14.....	38	22	58	304	13.8	27.3	23.4	2.6	12.5	34.2
F15-M15.....	39	26	66	295	11.3	26.5	29.1	4.1	15.9	24.4
M16-A15.....	20	20	100	261	13.1	36.4	47.9	0.4	4.9	10.3
A16-M15.....	40	36	90	411	11.4	44.5	47.2	0.7	0.9	6.6
M16-J15.....	60	40	67	584	14.6	28.1	25.2	1.0	4.3	41.4
J16-J15.....	27	18	67	212	11.8	17.5	22.2	6.1	8.0	46.2
J16.....	10	4	40	15	3.7	20.0	46.7	0	0	33.3
	437	266	60.9%	2696	10.1	33.4%	34.6%	1.9%	6.2%	23.9%

FIG. 1. Seasonal rates of infestation of meadow voles by *Hoplopleura acanthopus* and of deer mice by *H. hesperomydis*.

month to month also. Simultaneous analysis for differences between the sexes yield an  $F$  of 10.24 for meadow voles which is significant to the 1% level and for deer mice an  $F$  of 2.27 which is not significant. This further supports the contention that there is a real difference in rate of infestation between male and female meadow voles but none between male and female deer mice. The month to month variation in rate in both the meadow voles and the deer mice does show that the males and females fluctuate together (Figure 1) and that whatever is responsible for this fluctuation is probably the same in both sexes. This might indicate an extrinsic factor.

In order to determine whether or not the dif-

ferences in rate apparent between adjacent months are significant, a multiple range test (Snedecor 1956, p. 253) was used. This reveals significant differences from month to month to the 5% level. In the meadow voles there are no statistically significant differences during the July 1-August 15, August 16-September 15, and September 16-October 15 periods. However, the October 16-November 15 period shows a significantly higher rate. The following month (November 16-December 15) is significantly higher than October 16-November 15. The December 16-January 15 rate is lower, as is the January 16-February 14 rate. The former does not differ significantly from the peak rate (December 16-January 15) but the latter does, as does the February 15-March 15 rate. This winter low point is followed by a great increase in rate of infestation from March 16-April 15. This is followed by an increase to 100% in the April 16-May 15 samples. These two rates, while not significantly distinct from each other are distinct from the preceding rates and the rate for the May 16-June 15 samples. The final samples, June 16-July 15 and July 16-August 15, are neither significantly distinct from each other nor from the May 16-June 15 samples. It does seem from this that the high and low points in infestation rates are indicative of real seasonal changes in the rate of infestation in both sexes of the meadow vole.

In the deer mouse there also is seen to be significant variation between some periods. A multiple range test here reveals an increase in rate at a significant level over the preceding months sample in the October 16-November 15 sample and a significant decrease in rate over the preceding months sample in the January 16-February 14 sample. The latter is followed by an

TABLE VI. Infestation rate and population structure of *H. hesperomydis* on male and female deer mice per month

	Number Examined	Number Infested	% Infested	Total lice	Mean pop. size on infested hosts	ADULTS		NYMPHS		
						%♂♂	%♀♀	%3rd	%2nd	%1st
J16-A15.....	88	27	30.7	293	10.8	13.9	22.5	6.8	9.9	46.9
A16-S15.....	393	134	34.1	380	2.8	35.3	44.2	1.3	2.4	16.8
S16-O15.....	279	71	25.4	387	5.5	31.8	46.3	0.7	3.9	17.3
O16-N15.....	337	142	42.1	1078	7.6	25.7	38.1	1.9	8.3	25.9
N16-D15.....	269	112	41.6	702	6.3	30.5	45.7	2.7	6.7	14.4
D16-J15.....	73	29	39.7	166	5.7	37.9	34.9	1.2	6.0	19.9
J16-F14.....	38	9	23.7	37	4.1	32.4	62.2	0	2.7	2.7
F15-M15.....	21	10	47.6	23	2.3	26.1	69.6	0	4.3	0
M16-A15.....	50	17	34.0	107	6.3	27.1	57.0	1.9	4.7	9.3
A16-M15.....	104	18	17.3	83	4.6	37.3	45.8	6.0	2.4	7.2
M16-J15.....	129	37	28.7	313	8.5	25.2	42.8	5.7	6.4	19.8
J16-J15.....	70	21	30.0	133	6.3	24.8	39.8	1.5	6.0	27.8
J16.....	53	14	26.4	37	2.6	21.6	64.9	0	5.4	8.1
	1904	641	33.7%	3738	5.8	28.1%	41.5%	2.6%	6.4%	21.4%

increase and two successive decreases in rate in the samples, each of which is statistically significant. There are, then, in the deer mouse also two peaks in rate of infestation and a winter low point. However, the fall peak in the deer mouse precedes the peak in the meadow vole by one month and the winter low point also is one month ahead of the low point in the vole. The late winter peak in the deer mouse occurs at the same time that the winter low occurred in the vole. In addition, the rate dropped rapidly in the March 16-April 15 samples. The data do not reveal any significant changes after this period. There is, therefore, a seasonal variation in infestation rate as in the meadow vole, but it is somewhat less pronounced.

Seasonal changes in infestation rate have been suggested by Vysotskaia (1950) in his studies of *H. acanthopus* on *Microtus arvalis* near Leningrad in 1941 and 1945-46. He presents data which show a high rate of infestation in April followed by a period of low rate of infestation in June, July and August, followed by a second peak in September and October. Linsdale and Tevis (1951 pp. 155-162) in their study on the parasites of *Neotoma fuscipes* give tables and graphs on rate and intensity of infestations by *Neohaematopinus neotomae* throughout 1946 and part of 1947. The louse population of this rodent showed peaks in April and December. Elton, Ford and Baker (1931) have made a similar study of *Apodemus sylvaticus* harboring *Polyplax serrata* in England, but their data are grouped into quarterly samples. They show a maximum infestation rate of 30% in January-March, 1926, which is maintained through April-June, 1926 samples, and another peak was recorded in July-September, 1927.

In all of these studies the rate of infestation is lower than that found on our meadow voles al-

though somewhat similar to that found on our deer mice. However, it is not possible to make direct comparisons since collecting techniques differed.

#### Year to Year Variation in Rate of Infestation

In our study the percentage of infested meadow voles in July 1955 was significantly higher than in the same period in 1954 (Figure 1 and Tables IV and V). This year to year variation is not evident in the deer mice (Figure 1 and Table VI) when the data are analyzed.

Variation in infestation rate from year to year in various rodents has been noted by Vysotskaia (1950), Linsdale and Tevis (1951), Elton, Ford and Baker (1931) and Cook and Beer (1955). It is evident that there are definite fluctuations in the rate of infestation from year to year in the meadow vole, but this is not evident from our present deer mouse data.

#### Rate of Infestation with Age of Host

In the male meadow voles an increasing rate of infestation is evident in the older animals. In our samples, the nestlings and young mice 15-24 days of age have a rate of 65.1 and 61.9% respectively. This rate increases with age to a maximum of 94.9% in the 43-51 day old classes. The rate remains high in older animals. When the correlation of the age and rate of infestation is analyzed, an *r* of 0.854 results. With 5 degrees of freedom, this would indicate significance to near the 1% level. It is evident, then, that there is a positive correlation between age and rate of infestation in male meadow voles with the older animals having higher rates than the younger.

In the female meadow voles, on the other hand, there is little evidence of any change in rate with

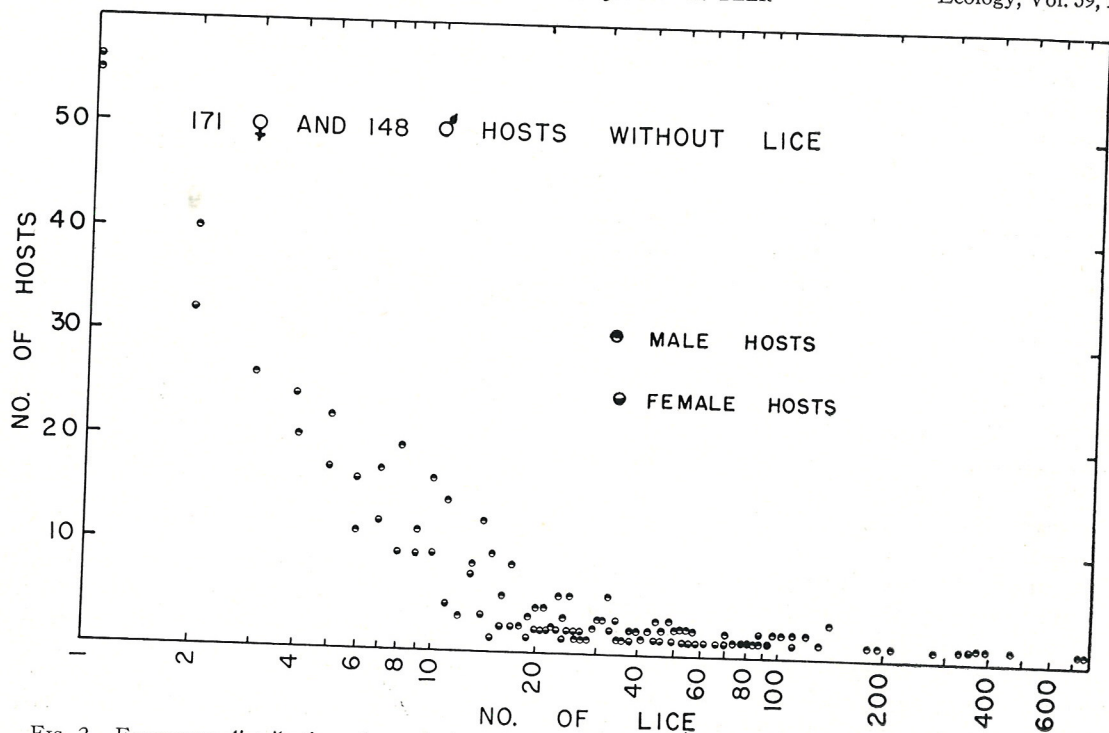


FIG. 2. Frequency distribution of population size classes of *Hoplopleura acanthopus* on meadow voles.

age (Table II). The rate varies from 53 to 67% with the correlation coefficient ( $r$ ) of  $-0.282$  indicating no evidence of correlation.

There is no evidence of increased susceptibility to louse infestation in the larger or older deer mice (Table III). Since no significant differences are apparent between male and female deer mice in regard to infestation rate and size, the data for males and females are here combined. A Chi-Square analysis of the infestation rates on various size classes of the deer mice result in  $\chi^2 = 9.77$ . With 8 degrees of freedom this gives a  $P = 0.25$ , which supports the conclusions that there is no significant difference in the rates observed on the various size classes.

#### Size of Infestation

The number of lice on any one infested meadow vole varied from one to 748 on the males in our sample, and the range on the females was from one to 354. The difference between the louse populations on male and female meadow voles is clearly shown in the average size of louse populations on the infested host. Of the total of 12,550 lice, 9,854 were recovered from 394 male meadow voles for an average of 25.1 lice per infested host while 2,696 lice were recovered from 266 female meadow voles for an average of 10.1 lice per infested vole. An analysis of variance of the mean size of infestation carried out for variation by

month and by sex yields an  $F$  of 9.27 for variation due to sex. This is significant at the 1% level. Only 59 of the 394 infested male meadow voles, or 15%, had populations of as large as 32 or more lice per host. Only 34 of 266, or 12.7%, of the infested females had more than 20 lice. The average population, then, is strongly skewed by a small number of meadow voles with very large louse populations. This can be seen in Figure 2. Actually, the 59 males with 32 or more lice each harbored more than 80% of all the lice recovered from males. In our present study, 19 males and two females (or 4.8 and 0.7% respectively), had 100 or more lice. In our studies on meadow voles in the Basswood Lake area already reported (Cook and Beer 1955), four of 43 infested males had more than 100 lice in the 1952 samples; one out of 53 infested females had more than 100 lice in 1952; and one of 22 infested males had in excess of 100 in 1953. Thus, of 454 infested male meadow voles from Basswood Lake and Rosemount, from 1952 through 1955, 24, or 5.3%, have had more than 100 lice. These larger populations, then, occur on a significant proportion of the male meadow voles and cannot be ignored. Of the 19 male meadow voles in our present study with over 100 lice, 17 were large and reproductively active specimens. The two non-reproductive specimens were taken in the March 1-15 collection. Of the remaining speci-

mens, six were taken in April, three in May, one in June, one in July, one in September, four in October, and one in November. Altogether, these 19 meadow voles harbored 5,048 lice or 51% of the total population on males.

That there may be a relationship between reproductive condition of the male host and the size of the louse population it harbors is suggested. Three size classes in parasite populations are recognized on the male meadow voles. The first class (which seems to constitute a distinctive group) is made up of those mice without lice; the second (which we consider to be more typical) is made up of those with from 1-31 lice; the third group is composed of those mice with 32 or more lice. The choice of 31 in the male meadow voles as the maximum number in the typical group was based on the fact that there is a break at this point in the curve plotted on Figure 2. Only 25% of the louse-free male meadow voles were reproductive, 40.5% of those with 1 to 31 lice were reproductive and 71.8% of those with more than 32 lice were reproductive forms.

There is no evidence that the meadow voles harboring these large populations had any pathological condition. From their size and weight data all were apparently healthy. Since the voles harboring these large louse populations form a constant part of the population and since these large populations are most often present on large, reproductively active, and apparently normal males, we have included them in the totals from which our mean population sizes are derived, despite the skewed effect that their inclusion may create. Even if the 19 male meadow voles harboring 100 or more lice were eliminated the seasonal picture is not fundamentally modified from that shown in Figure 3. The peaks are considerably reduced but the same general fluctuations are still apparent.

It is evident from Figure 2 that slightly more than 40% of the male meadow voles harbor from one to five lice, 60% have ten or fewer lice, and 77.4% have 20 or fewer lice. In the case of the female meadow voles, 58.2% have one to five lice, almost 79% have ten or fewer, and 89% have 20 or fewer. Since fewer female hosts harbor large populations and since the maximum population on females is lower than on males, the skewed effect on the mean of the louse population is probably smaller in female than in male hosts.

The number of lice on the infested host specimens varied from 1 to 104 in the male deer mice and from 1 to 165 in the females (Figure 4). There was little difference between louse population sizes on the two sexes. A total of 2,178 lice

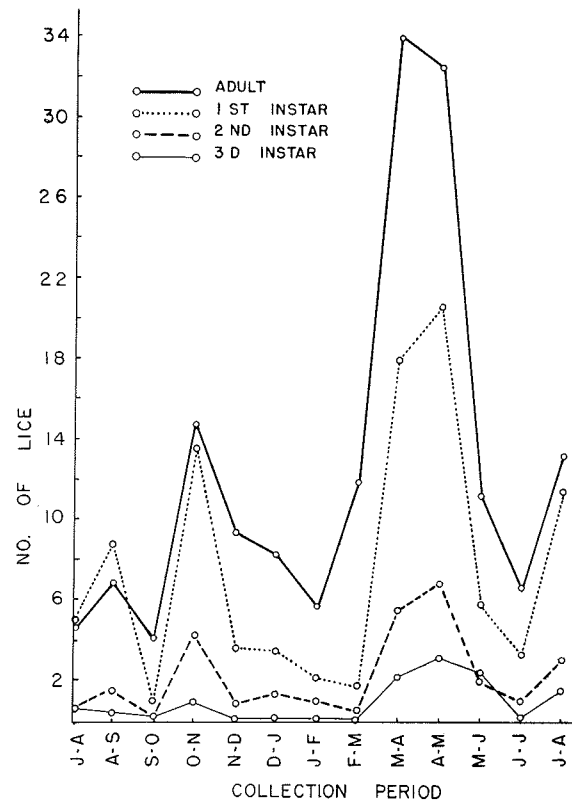


FIG. 3. Seasonal change in population size and structure of *Hoplopleura acanthopus* on male meadow voles.

were recovered from 381 male deer mice for an average of 5.7 lice per infested deer mouse. A total of 1,560 lice were recovered from 260 infested female deer mice for an average of 6.0 lice per infested mouse. The variation in mean infestation size due to sex gave an F of 2.27 which is not statistically significant. The average infestations found here are below those found on deer mice at Basswood Lake, Minnesota, during the summers of 1952 and 1953 (Cook and Beer 1955).

Only 51 of 381 infested male deer mice or 13.4% had populations of 10 or more lice, while 31 of 260 or 11.9% of the infested females had 10 or more. This small percentage of deer mice with 10 or more lice harbored 55% of the total lice recovered from males and 62% of the total lice recovered from females. Only two females and one male harbored more than 100 lice each. The male was an immature with 104 lice taken on October 27, 1954, and the females were subadult with 127 lice taken on November 11, 1954, and an adult with 165 lice taken on August 7, 1954. Seventy percent of the infested males had less than 5 lice each and 77% of the infested females had like populations. Population sizes are best understood by reference to Figure 4.

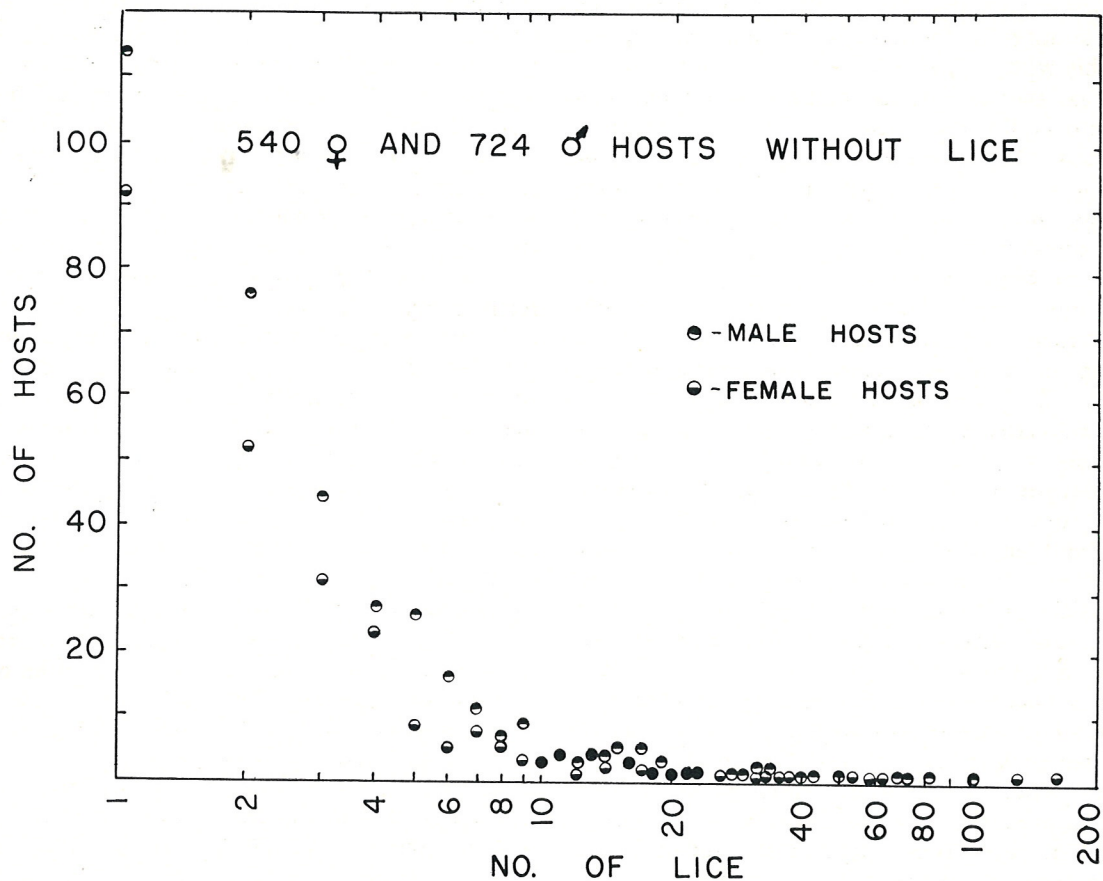


FIG. 4. Frequency distribution of population size classes of *Hoplopleura hesperomydis* on deer mice.

#### Variation with Season

The seasonal variation in the size of louse population on infested mice are evident in Figures 3, 5, and 6.

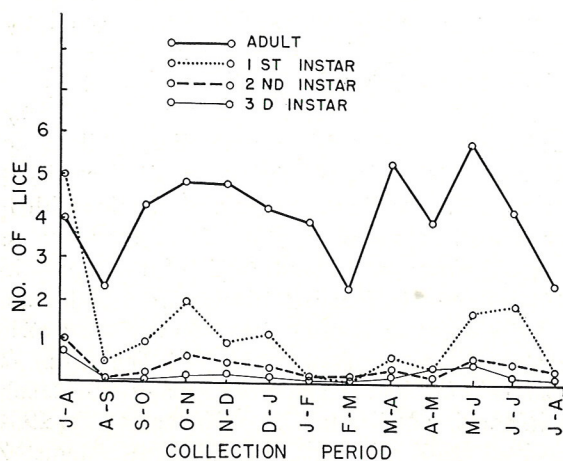


FIG. 5. Seasonal changes in population size and structure of *Hoplopleura acanthopus* on female meadow voles.

In male meadow voles (Figure 3) there is one conspicuous peak in mean population size covering

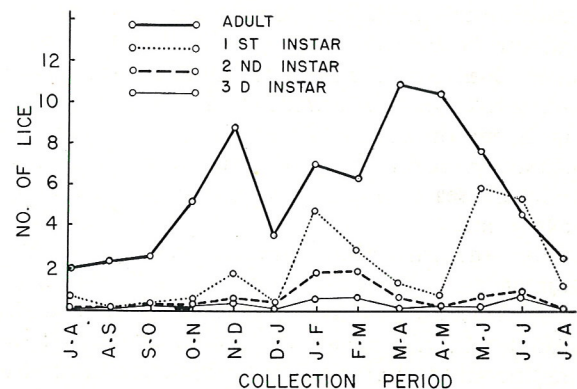


FIG. 6. Seasonal changes in population size and structure of *Hoplopleura hesperomydis* on deer mice.

the period from the last half of March through the first half of May. This peak in infestation size coincides with the period of maximum infestation rate for this species. In addition to the major peak there is a smaller one in the last half of October and the first half of November. The latter peak in mean size of infestation precedes the peak in rate of infestation by one month. The

period of declining population size from the end of November to the first half of February agrees roughly with the period of declining rate.

A variance analysis of the male infestation sizes alone over the year yields an  $F$  of 2.21 which is significant to the 5% level and very nearly to the 1% level.<sup>2</sup> Thus, there are definite seasonal changes in the size of the louse population on male meadow voles.

In the female meadow voles (Figure 5), with their much smaller infestation sizes, a major peak in population size is evident at the same period in the spring as in the males. This peak is much lower. The other major peak occurs in the fall a month later than in the males. However, an analysis of variance of the size of populations on females per month gives an  $F$  of 0.5 which is not significant. The coincidence of the peaks in the male and female population may be accidental and seasonal variation may not occur in the population sizes on female meadow voles, although the great similarity of the curves for males and females suggests that it does.

In the deer mice, the data for males and females have been combined as a consequence of finding no significant difference between the males and females either as to size of population or infested host or as to rate of infestation. In Figure 6 the variation in mean population size is given in our samples over the whole year. It would appear that there is a fall increase, a low point in the period from February 15 to March 15 and a spring increase roughly corresponding to that occurring in the voles. Analysis of the data, however, does not indicate that this variation over the whole year is significant in the deer mice. Thus, we do not know whether or not seasonal changes in population size occur in the deer mice, although seasonal changes apparently do occur in rate of infestation. Part of the difficulty here may lie in the inadequate sample sizes during the winter.

In the meadow voles the average louse population size in July, 1955, was somewhat larger than in July, 1954. Year-to-year differences have also been noted in samples from Basswood Lake, Minnesota, as recorded in our previous paper. Linsdale and Tevis (1951 Table 15 and Figure 69) also show year-to-year changes in population size as does Vysotskaia (1951). The differences shown in these studies are much greater than those found by us.

There is also some agreement between our data

<sup>2</sup> This analysis was based on the population of each individual host specimen rather than on the mean population per month.

and those of Linsdale and Tevis in regard to mean infestation size differences from month to month. In 1946 those authors show maximum infestations in February, April and June. Vysotskaia shows a spring maximum infestation in April, 1941, and in May, 1945. The latter author also shows a fall maximum in September and October. This agrees with our figures for male voles. Neither Linsdale and Tevis nor Vysotskaia distinguished between host sexes and, therefore, their data are not directly comparable to ours.

In our study, the spring maximum in the male meadow voles came at the period of greatest stress as far as the hosts are concerned. This was the period of general thaw when fields were extremely wet and the snow cover which had provided stability to the environment over the winter disappeared. Thus, the increase in the louse population size might result from lowered host resistance.

Vysotskaia (1950) indicates that the seasonal changes in the louse population are due to a variety of factors. The first factor which he considers to be important is the life cycle of the louse. This he seems to assume is quite long. The second factor is host molting which causes a large loss of eggs. He uses this to account for the small percentage of nymphs present in his April-to-August sample. We have found, on the other hand, that the largest proportion of immature lice is present in the period from July through October. New hair is growing in many of the mice through the summer but whether or not hair was being lost at the same time is unknown. A third factor is seasonal variation in host contact. He indicates that there is much contact in the spring which results in the large louse populations of the spring and that there is little contact in the winter which results in the low winter populations. We have no evidence of variation in host-to-host contact. The voles in the area of our study seem to be quite active during the winter as well as in the summer. Vysotskaia also indicates that there is competition between lice and other ectoparasites, such as ticks, fleas, beetles, and so forth. The infestations of mice by these parasites, he claims, reach a maximum in the period of October-November. This cannot be commented on as we have no quantitative data on other parasites. Finally, he claims that lice leave the host and live in the nest during the summer. This last assumption is most remarkable and apparently has never been noted in the literature elsewhere. No available reports on the fauna of mammal nests include records of live lice and, furthermore, most evidence

indicates that lice cannot survive for any great period off their normal host.

Linsdale and Tevis only make the statement that "wet weather seems to be conducive to the accumulation of lice by rats *Neotoma fuscipes*," by way of accounting for seasonal variation. This statement is not particularly well supported by their data.

#### *Variation with Age of Host*

The average size of louse infestation per infested meadow vole increases with successively older classes of males (Table I). The nestlings and the 15-24 day old mice have an average infestation of 11.4 and 10.0 lice per infested specimen. The average size of infestation increases to a high of 113.5 lice per infested male meadow vole in the 52-60 day age class and declines to 61 in the 60 day and older class. The last two samples are small in size (only 11 specimens each) and the extreme high may be due to sampling error. However, correlation of mean population size and age gives an  $r$  value of 0.773. With 5 degrees of freedom this is significant to the 5% level.

In the females an entirely different picture is apparent (Table II). The initial infestation of nestlings and 15-24 day old female meadow voles is 6.6 and 11.7 lice per infested vole. This is quite comparable to the infestation in the males in the same age classes. There is no constant increase in average infestation in successively older age classes and no suggestion of correlation is revealed by analysis.

The average size of the louse population on deer mice in our samples (Table III) shows little variation among the various size classes, and there is no evidence that the differences that are apparent are significant.

The period of greatest louse population size in male meadow voles coincides with the period in which the largest percentage of fully mature male hosts were present in the mouse population, *i.e.*, in April. It was felt that this April maximum in population size might merely reflect the greater number of mature mice that normally harbor large populations at this period. However, other peaks in average population size do not coincide with peaks in the percentage of mature males in the population. Therefore, the seasonal changes appear to be real although the height of the April peak is certainly enhanced by the larger percentage of mature males collected.

The great disparity in infestation rates and density between the male and female meadow voles has been noted in our previous paper (Cook and Beer 1955). Worth (1951) and Morlan and

Utterback (1952) have also noted the difference between male and female rodents in percentage of infestation. They have not recorded any differences in the size of infestations, which are even more marked. The suggestion has been advanced that the small louse populations of the female voles are due to migration of the lice from the females to the young in the nest, but a comparison of lactating females with those in which the mammae were undeveloped revealed no significant differences. It is true that the young may acquire a louse infestation at a very early period. Holdenried *et al.* (1951) note that young, hairless *Microtus californicus* in the nest were sometimes infested with lice. Linsdale and Tevis (1951), on the other hand, state that in *Neotoma fuscipes* the lice do not always transfer from the mother to the young even though the mother may have a heavy infestation. The difference between male and female voles is even more puzzling in light of the lack of such a difference in the deer mice infested by lice of the same genus.

Without more information on the life cycle, longevity, and reproductive capacity of the lice and more information on the biology of the host, any attempted explanation of seasonal and annual fluctuations and differences between sexes must be purely speculative.

#### *The Structure of the Parasite Population*

The seasonal changes in the louse population structure in meadow voles are shown in Tables IV and V and Figures 3 and 5. In total, there is a very low percentage of immature lice as compared with adult lice. In the males the overall structure of the louse population is comparable to that found on male meadow voles in the Basswood Lake area in the summers of 1952 and 1953. From the full year's sample (as compared to the Basswood Lake samples) we have a slightly lower percentage of first and second instars, a slightly higher percentage of adults, and the same percentage of third instars. In the females the full year's sample shows a structure intermediate between the two summer samples from Basswood Lake. There is a smaller percentage of immature stages than in 1952 but a larger percentage than in 1953.

The structure of the louse population on male and female deer mice over a full year is given in Table VI. Over the full year the percentage of immature lice was quite small, only 30.4%. This is an adult-nymph ratio of 1:0.43. This was considerably lower than that recorded for the two summers at Basswood Lake. In the male meadow voles the adult-nymph ratio was 1:0.87 and on

females 1:0.49. This ratio does vary seasonally but nymphs in the population never exceed 63% (or a ratio of 1:1.5) in the meadow voles or 43% (or a ratio of 1:0.75) in the deer mice where samples were adequate. This is far fewer nymphs than have been recorded in the case of human lice and a few other lice investigated previously (Hopkins 1949, MacLeod and Craufurd-Benson 1941). These authors cite adult-nymph ratios of 1:2.2 to 1:3.6. Vysotskaia (1950) presents an even lower adult-nymph ratio in *H. acanthopus* on *Microtus arvalis*. Of the 4,619 lice he recovered, only 921, or 19.9% were nymphs, a ratio of only 1:0.25. This could be the result of an inadequate technique for louse recovery.

In Figures 3 and 5 the seasonal changes in average infestations of meadow voles in our samples by various instars are illustrated. On the male voles all stages varied synchronously. The number of first instars only exceeded the number of adults at one point and the number of thirds only exceeded the number of seconds at one point. The number of second instars never exceeds the number of firsts. The synchronous variation of early instars and adults might be accounted for by a very brief duration for each nymphal instar. If a comparatively long period of development were required it would seem that a peak in first instars would be followed successively by peaks in the second and third instars and adults. On the female meadow voles, there is a much smaller nymphal population relative to that of the adults and considerably less variation is evident.

Vysotskaia (1950) has shown that the proportion of nymphs to adults varies with the season. In his samples the largest proportion of nymphs was found in April and December with no nymphs at all from June through August and only a small percentage in September and October. In our samples of meadow voles the percentage of second and third instars was relatively stable through the year on the male host (Table IV), and only marked by a single peak in March on the female host (Table V). The greatest changes occurred in the relative proportions of adults and first instars. In the males the largest percentage of first instars was present from July through October. This was followed by a steady decline in the percentage of first instars to a low point during the last half of February. Following this, there was an increase in first instars to a peak in April, a decline to a low in the last half of June and an increase again through July. The July, 1955 percentage of first instars approached that of July 1954.

In the female meadow voles the percentage of

the first instars was highest in 1954 in July. This dropped to zero in September. From that low, the proportion of first instars rose to less than 10% and remained relatively stable until January. At this point the percentages of both first and second instars rose, the first to a maximum in early February and the second to a maximum in March. These peaks were followed by a decline to a low at the end of April. After the April low the percentage of first instars rose to a maximum in June and remained stable through July.

In male and female deer mice (Table VI and Figure 6) the average numbers of second and third instars remained fairly stable and at a very low level throughout the year. In all but one period there were more second than third instars. The average number of first instars varied more widely, however, and more or less synchronously with the average number of adult lice. The smallest numbers of immature lice were present in the period of January 16 to May 15.

The relative proportions of the various instars through the year is evident in Table VI. The smallest percentage of immatures occurred between January 16 and May 15. This would seem to indicate a very limited winter reproduction in the louse populations. It would also suggest that survival of the louse population over this winter period might require adult lice with a life span greater than that usually attributed to them, *i.e.* 10-30 days (Hopkins 1949, p. 403).

#### *Variation in Population Structure with Age of Host*

On the male meadow voles the percentage of the louse population made up of second and third instars is relatively constant in all age classes of hosts while the percentage of first instars varies widely. The second instars vary only from 7.8 to 13.6% and the thirds vary from 1.8 to 10.3%. The maximum in the latter occurs in the 34-42 day old class. The greater part of the apparent variation in adult-nymph proportion is the result of differences in the relative proportions of first instars and adults. It is evident from Table I that the older male meadow voles have a larger proportion of nymphs than the younger. The correlation between age of host and percentage of nymphs gives an *r* value of 0.774 which is significant to 5%.

In the female voles (Table II), the nestlings and 16-25 day old mice have a similar population structure to that of the males of the same ages. From this age on, however, there is a decreasing proportion of nymphs with each successively older host class. Aside from the nestlings, the second

instars constitute no more than 8.5% of the louse population, the third instars never more than 2.1% and the first instars no more than 22.5% with the exception of the 52-60 day old class where it should be noted that a single female had 354 lice with a large percentage of first instars. As noted above, the nestlings and young mice from 16-24 days of age are directly comparable in louse population structure in both males and females, but following this period, in which both male and female hosts are similar in habitat, habit, and possibly physiology, the populations on the two sexes become strikingly different. The older classes of female hosts have a low and relatively stable proportion of the population made up of early instars rather than the successively larger proportion apparent in the males.

No significant relationship between deer mouse size and the age structure of the lice can be discerned (Table III). On the deer mice the largest percentage of immature lice was found on the 70-74 mm and the 95-99 mm classes. The 70-74 mm class is of adequate size but the figures are badly skewed by a single male with 104 lice of which 72 are first instars, 15 seconds, and 3 thirds. The 95-99 mm class is rather small and contains a single female with 165 lice of which 100 were first instars, 24 second instars and 15 third instars. The number of apparent nestlings that were infested was too small for reliable figures. The percentage of second and third instars was very low and relatively stable in all groups.

Four items are notable here: first, the stability in the percentage of second and third instars in both host species; second, the small percentage of these two instars; third, the small percentage of all nymphs when compared with adults; and fourth, the marked difference in the louse population structure and size between male and female meadow voles.

On the female meadow voles there is either relatively little reproduction of lice or reduced nymphal survival. This might account for the small population on the females as well as the smaller rate of infestation. The louse population of the female meadow vole might depend on continued re-infestation from the more heavily populated males. This is, of course, purely a speculation, since even lower infestation rates, densities and proportions of immatures occur on deer mice.

The small proportions of nymphs in our collection from both meadow voles and deer mice might be accounted for by postulating a relatively short duration for each early instar and a much greater longevity in the adults. It has been noted by Craufurd-Benson (1941) that the minimum dura-

tion for each nymphal instar in cattle lice is three days. The very small and stable percentage of second and third instars is rather puzzling. The percentage of first instars and adults fluctuates widely. It may be that these fluctuations represent variation in mortality as well as in reproduction, or both.

#### *Sex Ratio in H. acanthopus*

There is apparently little seasonal variation in sex ratio of *H. acanthopus* nor is there any very striking difference between louse sex ratio on male and female hosts. The percentage of male lice in the whole collection was 47.2.

#### *Sex Ratio in H. hesperomydis*

Over the whole year the adult louse population was made up of 40.3% male lice. This is a smaller percentage of males than that recorded for deer mice in two summer samples from Basswood Lake.

The greater percentage of female lice in adult populations is attributed to the greater longevity of the female by Craufurd-Benson (1941). The sex ratio we find is very different from that found by Vysotskaia (1950). Of a total of 3,698 lice collected by him, only 1,179 or 31.8% were males.

#### SUMMARY

1. In order to investigate populations of lice on cricetid rodents, populations of *Microtus pennsylvanicus*, the meadow vole, and *Peromyscus maniculatus bairdii*, the deer mouse, were sampled by trapping at two week intervals from July 1954 through July 1955. The twenty-five samples so obtained were grouped into monthly samples. These ranged in size from 56 to 132 meadow voles per month and from 21 to 393 deer mice per month. All data pertaining to each host specimen were recorded and the total louse population was recovered using a technique in which the host skin is dissolved and the parasites removed by straining through a 100 mesh bronze screen. The louse of the meadow vole is *Hoplopleura acanthopus* and that of the deer mouse is *H. hesperomydis*.
2. The infestation rate of meadow voles by *H. acanthopus* was found to be significantly lower in females than in males, but there is no such difference apparent in the infestation of male and female deer mice by *H. hesperomydis*. Meadow voles were found to be infested at a higher rate than deer mice in both sexes.
3. The rate of infestation varied significantly with the season in both meadow voles and deer mice although the variation is less striking in the deer mouse. High points in the rate in the meadow vole were in December and April and in the deer

- mice in December and March. This variation is comparable to that found in similar studies on other host species. Year to year differences in rate of infestation are also apparent in the meadow vole, but not in the deer mice.
4. The infestation rate in male meadow voles increased with increasing age. This is not true in female meadow voles nor in either sex in the deer mice.
  5. The average number of lice on male meadow voles was found to be considerably greater than on females, but there was no significant difference in the size of the louse populations on male and female deer mice. Meadow voles of both sexes had larger populations of lice than the deer mice.
  6. The average size of the louse population changed significantly with the season only in the male meadow voles. In the male meadow voles there was one major peak in population size in April and one lesser peak in October-November. In the females there seemed to be a major peak also in April and a lesser one in November-December. In the deer mice there seemed to be peaks in March-April, May-June and in November. The female meadow voles and the deer mice exhibited the same pattern as the male meadow voles in seasonal changes. Although statistical analysis did not reveal that the seasonal differences were significant here, the similarity in the high and low points of population size in the female meadow voles and the deer mice with the males, in which the changes were significant, would seem to indicate that seasonal changes do occur here also. This seasonal change in population size is comparable to that observed by other authors on other rodents. The spring maximum in the louse populations on the male host came at the period of greatest stress on the host (general spring thaw). Thus, population increase may result from a lowered resistance on the part of the host. The average size of louse infestations increased with age on the male meadow voles and a definite correlation is exhibited. Such is not the case in female meadow voles nor deer mice.
  7. Investigation of the structure of the louse population reveals a very small proportion of nymphs as compared to adults in both host species. In male meadow voles the adult nymph ratio was 1:0.87 and in the females 1:0.49. In deer mice the ratio for male and female hosts combined was 1:0.43. The proportion of second and third instars was low and stable throughout the year but the proportion of first instars to adults varied widely with the season. In general, early instars were more abundant on both hosts from April to October than from November to March. The largest proportion of nymphs were first instars followed by a much smaller number of seconds and very few thirds.
  8. There was a significant correlation between the proportion of first instars present and the age of the host in regard to the male meadow voles, the older males showing a much larger proportion of first instars than the younger. No such correlation was evident in the female meadow voles or the deer mice.
  9. The percentage of male lice from meadow voles was 47.2. On deer mice the percentage of male lice was 40.3. There seemed to be some fluctuation in these ratios but it was not significant.

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