THE BLACK FIELD CRICKET, AN INTERMEDIATE HOST FOR *MONILIFORMIS CLARKI* (ACANTHOCEPHALA)

by

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INTRODUCTION

The family Moniliformidae of the Archiacanthocephala which contains all the acanthocephala found in terrestrial mammals of North America, includes only a single genus, *Moniliformis*. The genus includes two species which occur in North America. One, *Moniliformis moniliformis*, has attained practically a worldwide distribution, while the other, *M. clarki*, is indigenous to North America. Cockroaches serve as the intermediate host for the cosmopolitan *M. moniliformis* which occurs as an adult in the intestine of the old world rats. North American squirrels are the chief definitive host for *M. clarki*. The intermediate host for this form has not been reported in the literature.

During the course of this study, some very exciting interrelationships between the population dynamics of the parasite and its hosts were discovered. Evidence of this sort, as presented below, opens up a relatively unused avenue of approach to the determination of an intermediate host. The usual method of placing the main emphasis on the laboratory determination of the physiological compatibility of the forms concerned leaves much to be desired, if one wishes to determine the particular host or hosts that are actively involved in seeing the parasite through the rigors of early life. Needless to say, physiological compatibility is essential, but the fact that a parasite is capable of developing in a particular form does not preclude the possibility that the parasite is actually utilizing a different host because of some ecological factor. Since very little is known about most acanthocephalan life cycles, the host specificity attributed to the larval forms may by the result of lack of information. The adult form of this parasite has been reported from five families, comprising three orders of mammals.

Evidence will be presented below to show that the common black field cricket *Acheta assimilis* (Fab.), is the intermediate host of *M. clarki* that parasitizes *Neotoma abigula* in the vicinity of Tucson, Arizona. Evidence from the literature clearly indicates that the cricket may be involved in other areas as well.

Chandler (1947) reporting on *M. clarki* in North American squirrels in Florida, stated that there seemed to be a correlation between the incidence of *M. clarki* in gray squirrels and the ecological habitat of the host. Of the eight squirrels collected in the river swamp association, none was parasitized. However, all three of the adults collected in the xeric association were infested. The river swamp contained a dense jungle-like growth with much of the ground covered with water most of the year (cf. also J. Moore, 1946). The xeric associations were dry with sparse undergrowth. Therefore, Chandler concluded that the intermediate host was limited to the drier localities. Also, Chandler (1942) failed to find *M. clarki* in a series of 12 fox and 4 gray squirrels collected in swampy woods in southern Texas.

Cantral (1943) working on the ecology of the Orthoptera of the George Reserve in Michigan, found that crickets may live close to the margin of swamps and marshes, but very rarely enter hydric habitats. This would explain why Chandler failed to find M. clarki in squirrels in the swampy areas of Texas and Florida, if the cricket is the intermediate host in those areas.

M. clarki is primarily a parasite of North American squirrels. The parasite has been reported from five of the genera of Sciuridae: Sciurus, Glaucomys, Tamias, Eutamias, and Citellus. The habit of foraging on the ground would bring squirrels into contact with the crickets. Although the cricket is considered to be nocturnal, on warm, moist days, they are active until late morning. I have heard them as late as 10 o'clock. Also, under the right conditions of moisture and temperature, the crickets become active early in the evening. This early morning, early evening activity of the crickets would overlap with the activity of the squirrels. Moore (1947) noted that Glaucomys, the Florida flying squirrel, foraged on the forest and in several cases found nests below the ground level with radiating tunnels.

ACKNOWLEDGMENTS

Many of the specimens examined during the course of this study were collected by or with the assistance of Keith E. Justice. For assistance in recording and tabulating data, I wish to thank Marilyn Hanemann. Also, I gratefully acknowledge Joe T. Marshall, Jr. for the encouragement and advice offered during the early phases of this study. I wish to particularly acknowledge the guidance and assistance of Albert R. Mead.

METHODS

The woodrats used in this study were obtained by Keith E. Justice and/or me by digging out dens or trapping. The woodrats were taken to the laboratory and examined for the adult form of Moniliformis clarki. The worms from parasitized woodrats were placed immediately into tap water to be relaxed for a period of 8 to 10 hours, or until they everted their proboscis. After the worms were completely relaxed, they were fixed in alcohol-formol-acetic acid (a. f. a.) after the formula of Cable (1953). The worms were left in the fixative for varying lengths of time, from overnight to a week, and then transfered to 70% alcohol for storage.

The crickets examined for the larval form of the parasite were obtained from dens of woodrats. Approximately 35 dens were dug out for that purpose. The crickets were collected in wide mouth jars and transported to the laboratory for examination.

In the laboratory, the crickets were anesthetized, and their heads and legs were trimmed off. A slit was made down the midventral line of the body and the larvae were washed out into saline solution (0.7% NaCl) with a small pipette. It was necessary to tease the crickets apart to find the larve adhering to the adipose tissue and the malpighian tubules. The gut was dissected out in its entirety and examined for the larvae in the process of passing into the haemocoel from the gut cavity. The larvae to be stained were treated by the same method used for adults. The examination as described above was carried out with the aid of a dissecting binocular scope and is essentially the procedure followed by Moore (1946).

The crickets to be infested artificially with eggs from adult worms were collected in front of food markets at night. They were placed individually into pint mason jars and were deprived of food for 24 hours. Pablum, infected with a suspension of eggs stripped from the body cavity of adult worms, was provided for each cricket on a small piece of glass slide. After several days, the crickets were placed into aquaria. The aquaria were provided with sand, paper toweling and a continuous supply of both food and water.

Woodrats reared in captivity were infested with larvae obtained from the haemocoel of crickets. Three methods were used in attempting artificially to infest woodrats. The first consisted of anesthetizing the animal and administering the larvae orally with a small pipette. This method was awkward in that it was difficult to determine how many of the larvae were swallowed, if any. The second method consisted of trimming off the jumping legs of the cricket, and putting the woodrat and the cricket together in a cage out of which the cricket could not escape. It is impossible with this method to determine the number of larvae infesting a cricket, if any. W. J. McCauley (oral communication) suggested the third method. A one-half inch wooden dowel, with a small hole through the center about three inches from one end that is tapered to a blunt point, was forced between the jaws of the animal to be infested. The dowel was rotated to roll out the tongue. A small catheter was inserted through the hole in the dowel and into the stomach of the woodrat. The larvae were injected directly into the stomach through the catheter with a small syringe. The syringe and tube were immediately washed out in saline solution to recover any larvae adhering to them.

The captive woodrats were provided with a constant supply of a standard rat diet (Purina laboratory chow). Moisture was provided in the form of prickly pear stems. In addition, a salt lick was provided each rat. The woodrats appeared to thrive on this diet. One male woodrat was kept almost two years on this diet, and appeared in excellent health when sacrificed.

The precipitation data were taken from the report of the U. S. Department of Commerce, Weather Bureau on local climatological data. The precipitation data were gathered at the Municipal Airport in Tucson, Arizona (U. S. Department of Commerce, Weather Bureau).

The staining procedure followed is that recommended by Van Cleave (1953). After staining, the specimens were dehydrated in successive changes of alcohol, increasing in strength with each change. Benzene was used to clear the specimens, and they were mounted in permount (Fisher).

Three stains were used: Semichon's carmine (Cable, 1953), borax carmine, and Erhlich's haematoxylin aged with potassium permanganate (Watson, 1943).

A large number of female worms were measured for total length. Total length is used as a rough estimate of age to determine the population structure of the adult parasite for the various months of the year. All other measurements taken on both the adults and the larvae were taken with an ocular micrometer.

RESULTS

Woodrat Infestations

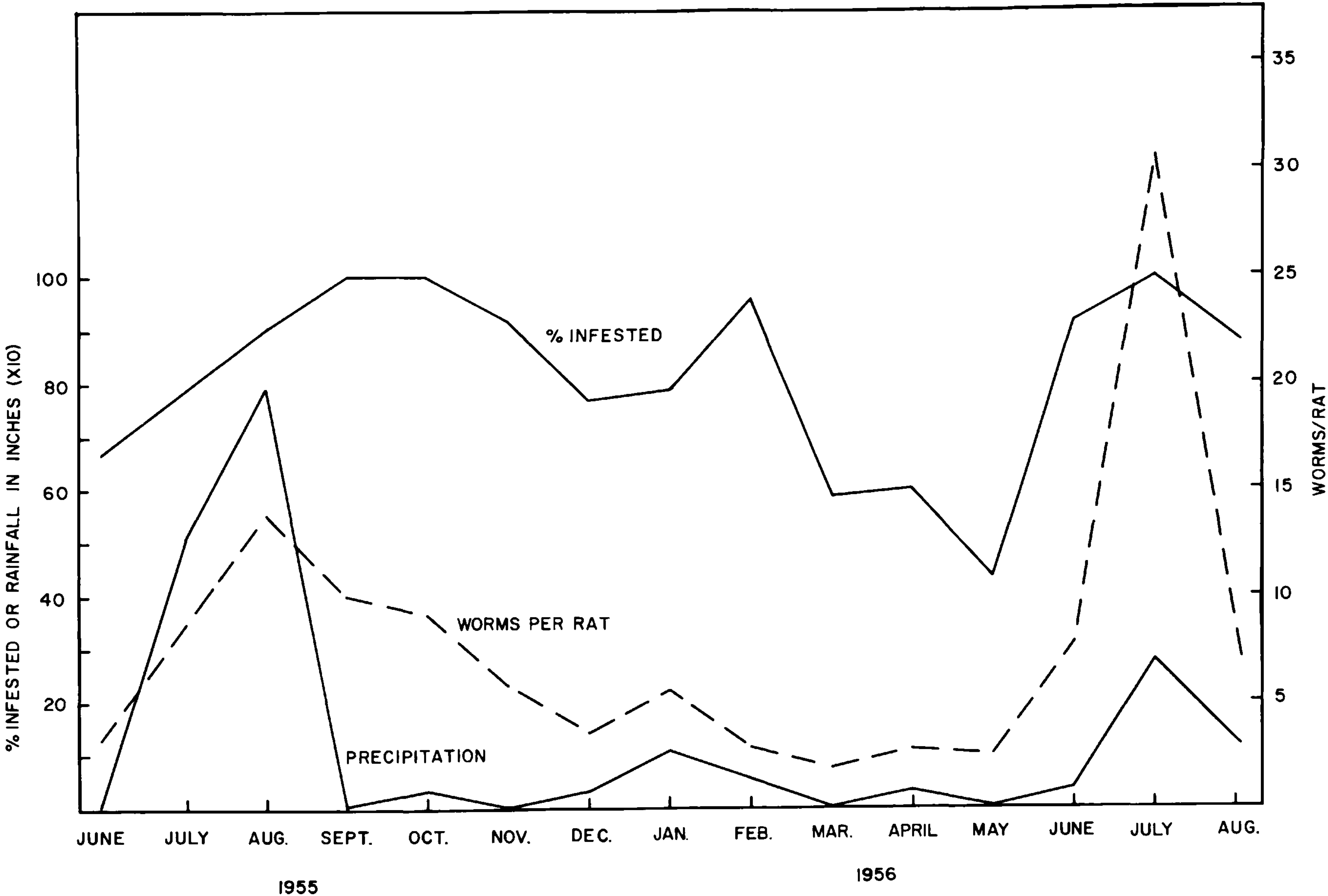
In the study area, 10 miles east of Tucson along the Old Spanish Trail, better than 50% of the woodrats are infested with the acanthocephalan, *Moniliformis clarki* throughout the year (Fig. 1, Table 1). It is evident that there are two peaks each year in the infestation, one at the end of summer and the other around the first of the year. Although the percentage infestation approaches 100% in each case, the late summer peak represents a much heavier infestation per rat. The number of worms per rat represented by the July, 1956, peak is more than five times the number for the January, 1956, peak. Data for July, 1955, are lacking, but the infestation in August, 1955, is more than twice that in January, 1956.

There seems to be a good correlation between the amount of infestation and precipitation. In 1955 and 1956 the summer rains are followed closely by both an increase in the percentage infestation and in the number of worms per rat. Also, there is a similar increase, although not as prominent, after the winter rains early in 1956. This correlation appears to be a consequence of the role which rainfall plays in the interrelationship between the woodrat and the intermediate host.

Fig. 1. The rate and incidence of infestation of Moniliformis clarki in the woodrat as correlated with precipitation (infestation data for July, 1955, is missing).

Table 1.--Monthly data of precipitation and woodrat infestation (T = trace).

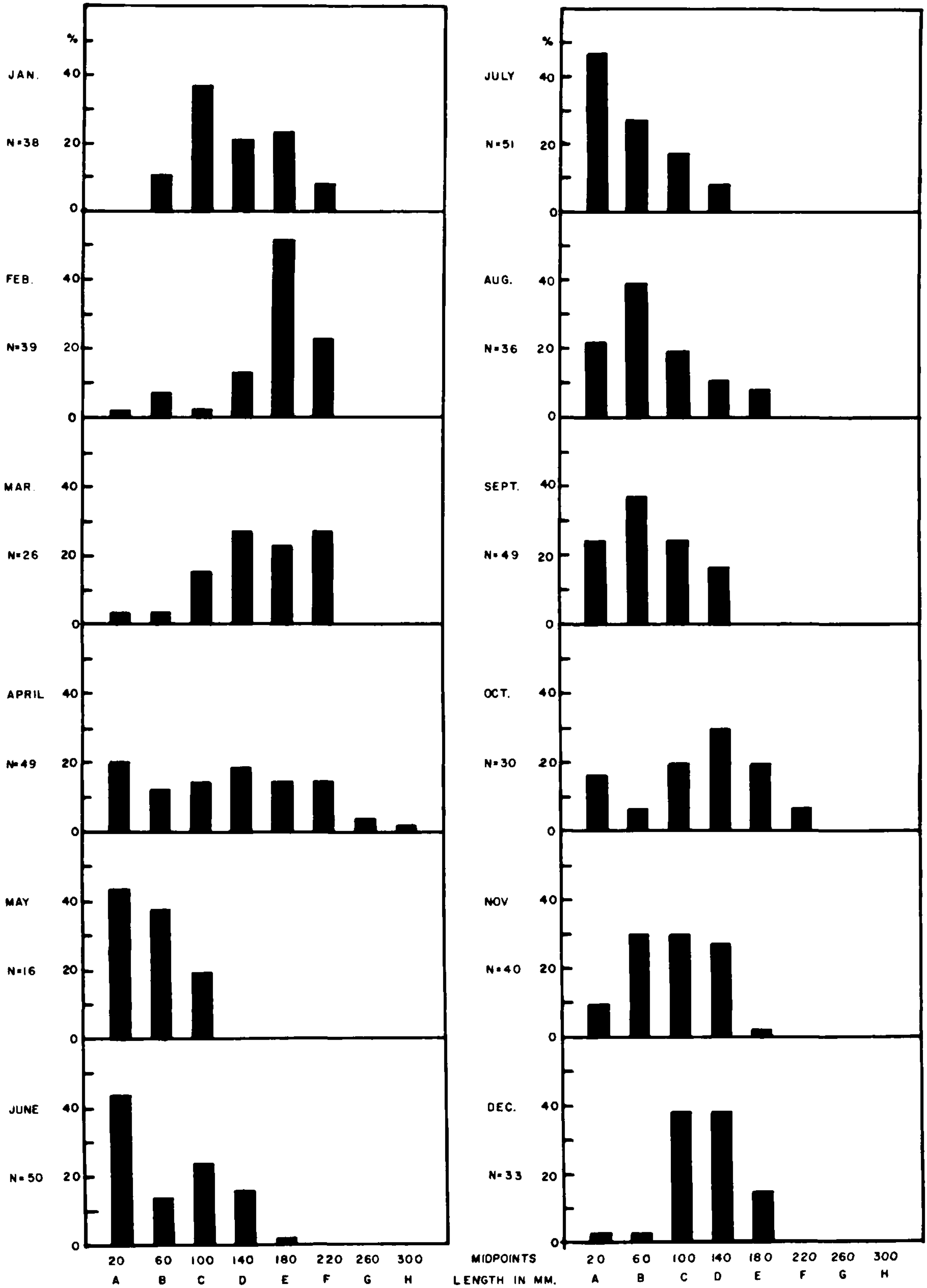
Year	Month	Number of rats (N)	Number of rats infested	% of rats infested	Worms per rat	Maximum	Precipitation
1955	June	12	8	66.7	3.18	12	0.03
	July						5.10
	Aug.	92	83	90.2	13.80	131	7.93
	Sept.	4	4	100.0	10.00	41	0.05
	Oct.	15	15	100.0	9.07	35	0.32
	Nov.	24	22	91.7	5.75	33	T
	Dec.	13	10	76.9	3.55	13	0.33
1956	Jan.	14	11	78.6	5.79	42	1.08
	Feb.	22	21	95.5	2.82	12	0.54
	Mar.	31	18	58.1	1.93	12	0.00
	Apr.	35	21	60.0	2.71	14	0.31
	May	15	8	53.3	2.53	20	T
	June	23	21	91.3	7.79	31	0.36
	July	26	26	100.0	30.46	151	2.77
	Aug.	8	7	87.5	7.00	24	1.12


% INFESTED OR RAINFALL IN INCHES (X10)
100
80
60
40
20
35
30
25
20
15
10
5
WORMS/RAT
% INFESTED
WORMS PER RAT
PRECIPITATION
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MAR.
APRIL
MAY
JUNE
JULY
AUG.
1955
1956

To get some idea of the population structure of the worms throughout the year, a series of worms from each month was measured for total length. Only the females were measured, for two reasons. There is a pronounced sexual dimorphism for length, with the females as much as two or three times the length of the males. Further, the males appear to be eliminated from the woodrat earlier than the females. In this work, length is used as a rough estimate of age, with full knowledge of the fact that Burlingame and Chandler (1941) have shown that total length is dependent on a number of factors, such as the amount of infestation and position in the intestine. At present, size seems to be the best indication of age available.

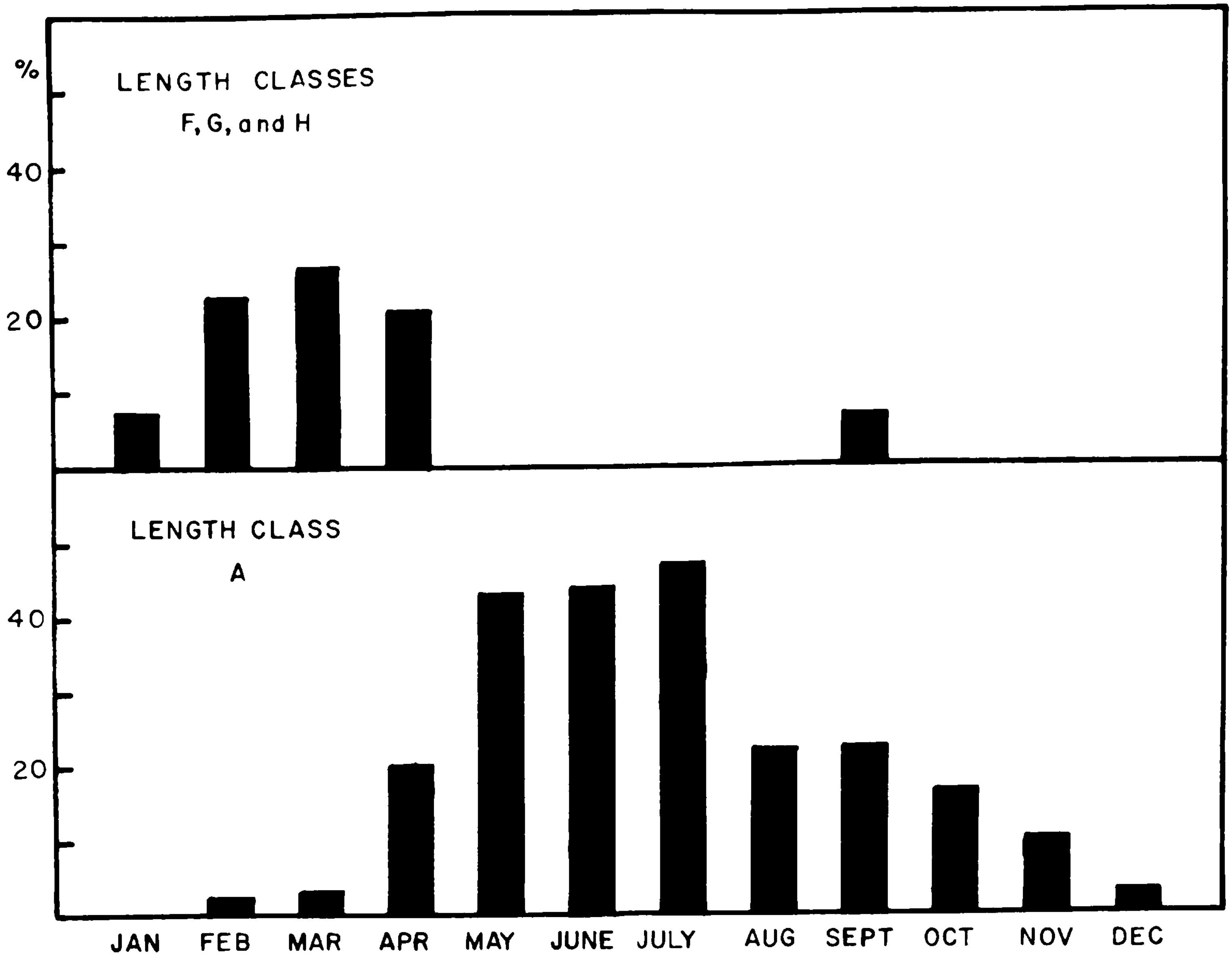
The worms were grouped into eight classes according to length. The first class (class A) contains worms 1-40 mm. in length, the second 41-80 mm., and so forth to class H which contains worms 281-320 mm. long. The percentage frequency distributions for each month of the year are represented by the histograms in Fig. 2. In each case, N represents the total number of worms measured for that month. The number of rats represented for each month, along with the other numerical data for Fig. 2, is given in Table II. The individual class A and the combined classes F, G, and H in Fig. 3 show graphically the percentage distributions of the classes comprising the smallest and largest worms, respectively, throughout the year.

Fig. 2. Monthly distribution of length classes of adult female Moniliformis clarki in the woodrat.



%
JAN.
N=38
FEB.
N=39
MAR.
N=26
APRIL
N=49
MAY
N=16
JUNE
N=50
JULY
N=51
AUG.
N=36
SEPT.
N=49
OCT.
N=30
NOV
N=40
DEC.
N=33
0
20
40
20 60 100 140 180 220 260 300
A B C D E F G H
MIDPOINTS
LENGTH IN MM.

Fig. 3. The distribution of the smallest (class A) and the largest (combined classes F, G, and H) adult female worms by monthly periods.



%
LENGTH CLASSES
F, G, and H
40
20
LENGTH CLASS
A
40
20
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC

Table 2.--Monthly data in the population structure of M. clarki as indicated by total length.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. rats	(10)	(17)	(11)	(13)	(6)	(7)	(4)	(5)	(6)	(7)	(4)	(8)
No. worms (N)	38	39	26	49	16	50	51	36	49	30	40	33
Range (length) mm.	72-222	24-232	34-233	15-296	8-119	4-173	4-152	2-202	8-146	8-201	17-152	38-178
No. worms in each length class and % of total in parenthesis												
0-40		1 (2.5)	1 (3.8)	10 (20.4)	7 (43.7)	22 (44.0)	24 (47.0)	8 (22.2)	11 (22.4)	5 (16.7)	4 (10.0)	1 (3.0)
41-80	4 (10.5)	3 (7.7)	1 (3.8)	6 (12.4)	6 (37.5)	7 (14.0)	14 (27.4)	14 (38.9)	18 (36.8)	2 (6.7)	12 (30.0)	1 (3.0)
81-120	14 (36.8)	1 (2.5)	4 (15.7)	7 (14.6)	3 (18.7)	12 (24.0)	9 (17.6)	7 (19.4)	12 (24.5)	6 (20.0)	12 (30.0)	13 (38.4)
121-160	8 (21.0)	5 (12.8)	7 (26.9)	9 (18.7)		8 (16.0)	4 (7.9)	4 (11.1)	8 (16.6)	9 (30.0)	11 (27.5)	13 (38.4)
161-200	9 (23.6)	20 (51.6)	6 (23.0)	7 (14.6)		1 (2.0)		3 (8.3)		6 (20.0)	1 (2.5)	5 (15.2)
201-240	3 (7.9)	9 (23.0)	7 (26.9)	7 (14.6)						2 (6.7)		
241-280				2 (4.1)								
281-320				1 (2.0)								

It is evident from the frequencies graphed that during the first three months, worms of intermediate size make up most of the population. In January, the smallest of the worms, class A, and the largest of the worms, classes G and H, are not represented. However, in February and March a few juvenile worms appear. Also, there is a shift of the frequencies toward the longer individuals, but still the last two classes are absent. It is not until April that the last two classes become represented in the population. Also in April, the first class (class A) has increased to slightly more than 20%. The increase in the extreme classes tends to flatten out the distribution for April.

By May a decided change in the population has occured. The entire population is made up of individuals falling in the first three classes only. The large worms have dropped out completely and the young worms have taken over. The heavy infestation with young worms is increased slightly in June, falls off slightly in July and then continues falling throughout the rest of the year. Along with the decrease in frequency of the young, there is a corresponding increase in the frequencies of the intermediate classes, but apparently no increase in the last three classes. Either the worms are being eliminated before they can reach the larger size, or because of environmental reasons, such as competition for food or space, growth is slowed at this time of year. It is not until January that class F begins to show up consistently and in any amount. From January on, growth in length continues, until the population turnover in May, at which time the old worms drop out to be replaced by the next generation.

It is clear from the evidence presented that there is a complete population turnover each year. The large adults from the previous year drop out completely at the time of the heavy reinfestations in May and June. This fact and the fact that the worms do not grow to an extremely large size until after the heavy reinfestation has ceased, indicate that the older worms are being pushed out by the constant reinfestation by juveniles. Burlingame and Chandler (1941), working with the closely related form Moniliformis moniliformis, found that after infesting rats with the larvae of this form and then superimposing another infestation on the first, there was a loss of worms from the initial infestation, as well as from the second.

Since all known life histories of acanthoceophalans are complicated by at least two hosts, a vertebrate species as a difinitive host and an invertebrate or vertebrate as an intermediate host, the occurence of the parasite at any time or place is dependent upon the concomitant occurence of both hosts. Therefore any intermediate host proposed for Moniliformis clarki must fulfill certain qualifications. For example, it is apparent from the evidence presented, that the intermediate host must present a continuous source of infestation throughout most of the year. It must occur in fairly large numbers and be readily accessible as food to keep the tremendous infestation of the woodrat at such a high level throughout the year. As indicated before, the intermediate host must be sensitive to precipitation, or perhaps both hosts are affected by precipitation in some way. Since the percentage of juvenile worms drops off practically to zero the last of the year and the first of the next, the intermediate host must be correspondingly inaccessible to the rat at that time. The percentage infestation of the intermediate host also may be low at that time. However, since the female worms are adult and gravid, the evidence would seem to point to the intermediate host being in a less accessible form or stage in its development.

Cricket Infestation

The usual site of infestation of adult acanthocephalans in land mammals is in the lumen of the small intestine. Here fertilization takes place and fully embryonated eggs are shed by the worm which pass to the outside in the feces of the host. A suitable intermediate host, usually an arthropod, feeding on the feces or material contaminated by the feces, ingests the eggs. The eggs hatch, releasing the acanthor, the newly hatched larva, into the lumen of the midintestine. After ten or more days, the acanthors work their way through the wall of the intestine. They drop into the cavity of the haemocoele, encyst in a hyaline sheath, and complete development to the infective stage in from four to eight weeks (Burlingame and Chandler, 1941; D. Moore, 1946). The cycle is completed when the definitive host eats the infested intermediate host. It was with these thoughts foremost in mind that an attempt was made to discover the intermediate host or hosts that are maintaining the heavy infestation of the parasite in the woodrat in the study area.

From field observations and evidence presented by Justice (1956), the woodrat appears to be a rather sedentary animal, spending most of its time in the den or in its vicinity. Therefore, the search for the intermediate host was started by examining the various arthropods found in or around the dens of woodrats. Of the various forms examined, only the black field cricket was found infested with the larval stage of *M. clarki*. The larvae in the cricket were identified as *M. clarki* on the basis of the morphological evidence presented in Table 3, and the description of the adult worm by Van Cleave (1953).

The possibility that the grubs of certain winged adult arthropods may be serving as intermediate hosts has not been eliminated entirely. Only a limited number of arthropod grubs have been examined at this time.

It soon became apparent that the cricket is the most abundant and the most consistent inhabitant of the woodrat's den. Vorhies and Taylor (1940) found 55% of the dens with "one to several" crickets on the Santa Rita Experimental Range. I have found crickets in 100% of the dens in the study area. But two of the many dens examined 10 miles from Black Mountain, south of Tucson were found lacking crickets.

The abundance of the crickets depends upon the time of year the den is examined. The *adult* crickets first appear in the dens around the middle of June. In 1956, the first adults were collected on June 22, at which time approximately three-fourths of the crickets collected were adults. By the end of the first week in July most of the crickets had become adults. The nymphs started to appear again around the middle of August. Eleven small nymphs were collected from a den on August 17. Nymphs first appeared in cricket cultures in the laboratory on August 12. By the time of the first appearance of the nymphs, the adult population had dwindled to just a

Table 3.-- Morphological measurements of the adults and larvae of Monilitormis clarki, in mm., compared with those as reported for the adults by Van Cleave (1953).

Source	Proboscis length	Proboscis width	Hook length	No. Rows	No. Columns
Adults from woodrats	.22-.31	.12-.17	.019-.021	12-14	6-8
Larvae from crickets	.23-.28	.11-.14	.017-.021	12-14	6-9
Adults from literature	.28-.42	.11-.15	.016-.021	12-16	6-8

few individuals here and there. In eight dens examined after the appearence of the nymphs, only five adults were collected. The last adult was collected on September 8. One adult was heard on October 17, the last record of adults for the year.

It seems evident, therefore, that the crickets in the study area represent a single population that overwinters primarily in the nymphal stages. Ball et al. (1942) reported that at lower elevations both nymphs and adults are found all winter in considerable numbers. From observations made during this study, it would seem that overwintering adults are limited to areas where irrigation is practiced, such as lawns in town. Adults can be heard on any warm winter night around Tucson and especially on the campus of the University of Arizona.

Figure 4 shows both the percentage infestation of the crickets and the number of larvae per cricket. N is the number of crickets examined in each month. There is one peak occurring in the late summer which corresponds to the peak in the worm infestation (Fig. 2). This peak occurs just before the decline of the adult cricket population. The dropping off of the infestation in September is a result of the dying off of the adult crickets. Only one adult cricket was collected after August. It was infested with two larvae. The rest of the crickets of September and October were nymphs in the early instars. It should be noted that one nymph was collected in September and another in October that was infested with one and two larvae respectively.

The last column of Table 4 gives for each month the maximum number of larvae found in any one cricket. With the exception of May there is a steady increase from two in February to 54 in August. The evidence clearly shows that the heavy infestation in late summer is the result of two different factors, that is, an increase in the rate and a corresponding increase in the incidence of infestation in the cricket. That is to say, the woodrat would not have to eat any more crickets than usual to increase many fold the number of worms harbored.

Fig. 4. The rate and incidence of infestation of Moniliformis clarki in the black field cricket (data for 1955 and 1956 combined). N is the number of crickets examined in any month.

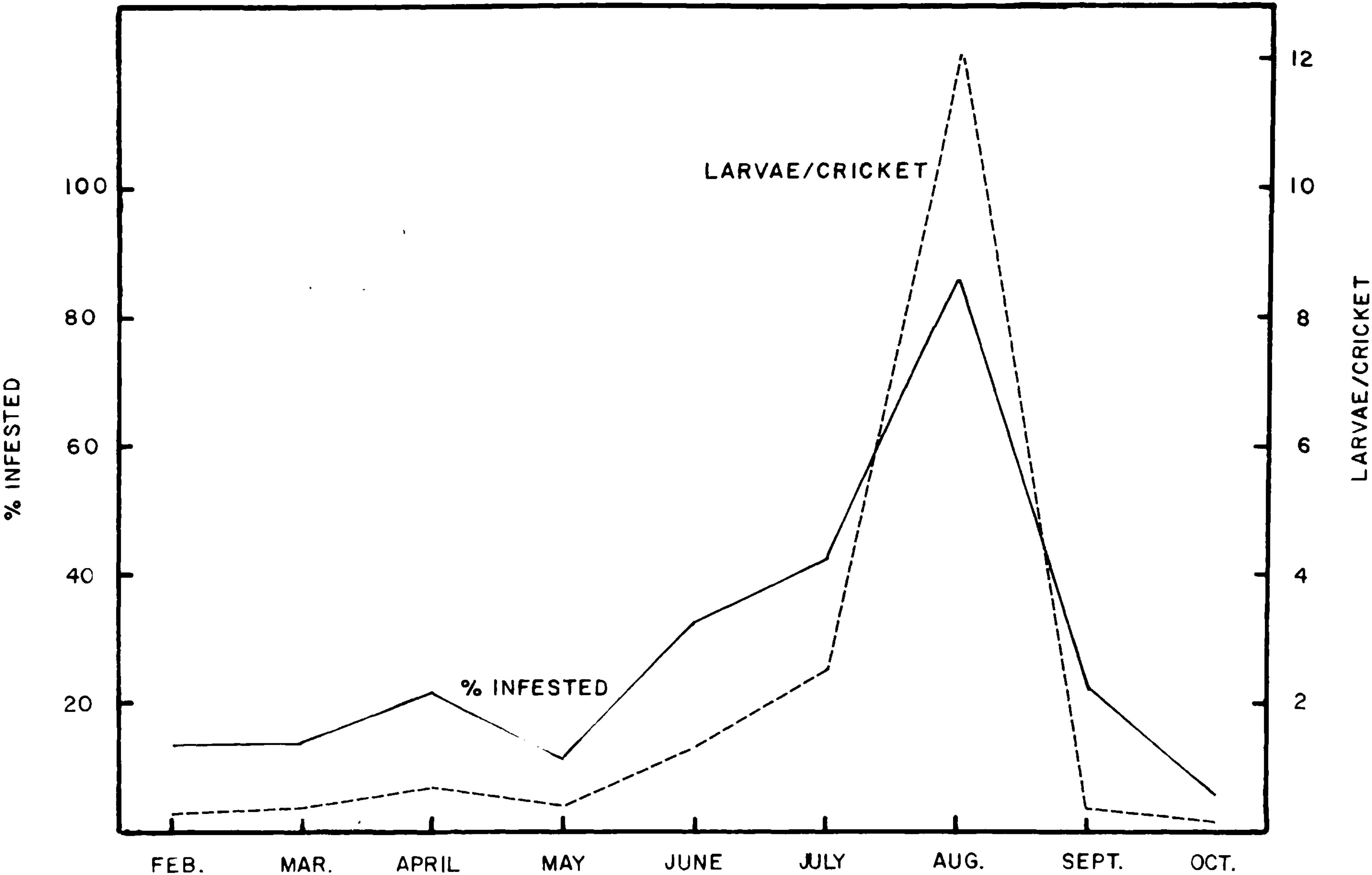

LARVAE/CRICKET
% INFESTED
% INFESTED
LARVAE/CRICKET
100
80
60
40
20
12
10
8
6
4
2
FEB.
MAR.
APRIL
MAY
JUNE
JULY
AUG.
SEPT.
OCT.

Table 4.--Monthly data of cricket infestation.

Months	(N) No. crickets	No. infested	No. larvae	% infested	larvae / cricket	Max.
1						
2	22	3	6	13.6	.27	2
3	22	3	8	13.6	.37	4
4	38	8	24	21.1	.63	8
5	18	2	7	11.1	.39	6
6	31	10	39	32.3	1.26	10
7	19	8	47	42.1	2.47	18
8	7	6	84	87.7	12.0	54
9	9	2	3	22.2	.33	2
10	17	1	2	5.9	.12	2

Artificial Infestations

The population of crickets within the city was sampled from time to time throughout the year and was found to be free of the larval _M. clarki_. From 45 to 50 crickets collected within the city, primarily around food markets in the evening and on the University campus, were infested as described under "Methods." Of these only 12 survived to be examined. The heavy mortality was apparently caused by injury sustained during capture and by cannibalism. Also, there is the possibility that the infestation may have been a contributing factor.

Of the 12 artificially infested crickets examined, 10 had the larvae of _M. clarki_ encysted in their haemocoele. The number of larvae in any one cricket ranged from 1 to 141 (Table 5). The large discrepancy in the range can be explained in part by the following facts. The crickets were infested with eggs stripped from the body cavity of worms late in July and early August. A glance at the graphs of Figure 2 shows that at that time of year, there were very few large worms available from which to obtain fertilized and fully embryonated eggs. Attempts to hatch the eggs by the method of Manter (1928), as improved by Moore (1942), proved disheartening in most cases.

Three methods were used in attempting to pass the infestation from the cricket to the woodrat. The first, by oral pipette, was completely unsuccessful (Table 5, Rat No.'s

Table 5.-- Upper: Data for the 9 rats artificially infested (see text for discussion). Lower: Cricket infestation data are presented for both the natural and artificial infestations.

Rat No.	No. larvae admin.	No. worms recovered	% recovery
1	8		
2	9		
3	9		
4	?	2	
5	?	4	
6	8		
7	18	4	22.2
8	15		
9	16	7	43.8

Source of crickets	No. crickets	No. infested	No. larvae	% infested	larvae / cricket	Max.
Town	12	10	203	83.3	16.9	141
Study area	183	43	220	23.5	1.2	54

1, 2, and 3). The second method (Rat No.'s 3 and 4), feeding live crickets to the woodrats, yielded the best results of the three. From the two rats fed crickets, two and four worms respectively were recovered. Each of the two woodrats had been fed three crickets. The third method (Rat No.'s 5, 6, 7, 8, and 9), injecting the larvae directly into the stomach by means of a catheter and syringe, yielded moderate results. Four worms were recovered after injecting 18 larvae into rat No. 7, and 7 worms from 16 larvae were recovered from rat No. 9. Rat No.'s 1 through 8 were woodrats born or raised from an early age in captivity, while rat No. 9 was a hooded rat which was also born and raised in the Laboratory. It was assumed that these animals were free of the infestation and therefore no prelimenary examination of the feces was made.

Rat No.'s 4, 5, and 9 were animals infested with the larvae of naturally infested crickets from the study area. Rat No. 7, however, was infested with larvae obtained from a cricket artificially infested with eggs from an adult worm. The two female worms from rat No. 7 were adult and contained fully embryonated eggs. These results show that the cricket is physiologically capable of being an intermediate host.

Discussion

The black field cricket appears to satisfy all the requirements for the intermediate host of Moniliformis clarki as it occurs in the woodrat in the vicinity of Tucson. Cantrall (1943) ranks the cricket as a scavenger. He reported crickets feeding upon various kinds of food including dead mice, dead insects, other crickets, and various vegetal materials. Folsom and Woke (1939) observed crickets eating both dried and green vegetal materials, moths, cockroaches, dead tiger beetles, and dead or dying crickets. They list the cricket as omnivorous. I have observed crickets eating various vegetal materials in the laboratory such as lettuce, cabbage, carrots, and apples, as well as each other. It seems highly probable the woodrat droppings or at least materials contaminated by woodrat droppings would comprise a certain percentage of the food of the cricket living in a den.

Both McGregor (1929) and Folsom and Woke (1939) reported that overwintering nymphs become active, feed, and molt on warm days. The fact that the nymphs of the study area get progressively larger toward spring would indicate that there is some activity during the winter. Also, on hot, dry nights the crickets stay within the confines of the den, but on warm (but not hot) moist nights, they are found as much as four feet away from the den.

It would seem then that this characteristic of the cricket to become active on warm, moist nights would explain the relatively small peak in the worm population right after the winter rains. If it is assumed that the main factor determining whether a woodrat will eat a cricket or not is frequency of encounter, then it would seem reasonable that if the cricket is out of the den actively feeding, an encounter would be more probable than if the cricket was lost somewhere in the debris of the den. Therefore, the winter peak in the infestation of the woodrat is not the result of either an increase in the absolute number or in the amount of infestation of the intermediate host, but rather to the increased frequency of encounter between the woodrat and the cricket.

It is also significant that the late summer peak follows the summer rains. This is the time of year that the crickets are molting into adults and actively engaged in breeding. Again there is an increase in the frequency of encounter between the woodrat and the cricket followed by the expected increase in the infestation of the woodrat. Recall, however, that the peak in the amount of infestation following the summer rains is more than five times the corresponding peak following the winter rains. It would seem unlikely that this tremendous increase of infestation in the summer could be explained solely by the increased activity of the cricket. The answer seems to be in the extensive increase in the amount of infestation in the cricket. Not only will the woodrats encounter and eat more crickets, but more of the crickets will be infested with a greater incidence of larvae than was the case in crickets eaten during the previous winter. Therefore, the summer peak is complicated by three factors acting simultaneously. That is, an increase in the activity of the crickets, an increase in the percentage or the spreading of the infestation within the cricket population, and an increase in the amount of infestation in any one cricket.

The factors affecting the buildup of the infestation in the cricket are not as apparent. If it is assumed that the infested nymphs live to become adults, then there would be a gradual increase in the amount of infestation in the cricket population with time. This would explain the gradual buildup, but not the blossoming forth of the infestation after the summer rains. Perhaps the rains cause contamination of the food used by the cricket. Then again, perhaps the woodrat droppings become more palatable after a rain.

Earlier in this paper it was suggested that perhaps the crickets are adversely affected by a heavy infestation of the larval acanthocephalans. It was concluded from data presented under "Results" that the decline in the amount of infestation in the cricket was the result of the dying off of the adult cricket population. It seems significant that no adult crickets were seen or heard after the middle of

October in the study area; yet, in town, adults can be both seen and heard on any warm night all winter.

The woodrat shows no outward sign of adverse effects that could be attributed to the parasite. This is very surprising indeed considering the extent of infestation during most of the year. The problem of host-parasite relations between these two forms is very interesting and needs further investigation.

Summary

The black field cricket, Acheta assimilis, is the intermediate host of Moniliformis clarki which parasitizes the woodrat, Neotoma albigula, in the vicinity of Tucson, Arizona. Evidence from the literature on the habits of the cricket suggests that it may be serving as the intermediate host in other areas.

Physiological compatibility between the parasite and the cricket was demonstrated by the recovery of mature adult worms from laboratory reared woodrats infested with larvae from wild crickets.

Evidence in the form of the interrelationships between the population dynamics of the parasite and its hosts, is presented to demonstrate that the cricket is actually the intermediate host in the study area. The need for more emphasis on the interrelationships between the parasite and its hosts is discussed.

There are two peaks in the incidence of infestation in the woodrat. One, a relatively high peak, follows the summer rains, and the other, a relatively lower peak, follows the winter rains. The winter peak is the result of a higher frequency of encounter between the lightly infested cricket and the woodrat following the winter rains. The summer peak is the result of three factors: an increase in the activity of the crickets following the summer rains, an increase in the percentage infestation in the cricket

population, and an increase in the amount of infestation per cricket.

The summer peak in the infestation of the cricket is, in part, an accumulation from the early instars. Also, perhaps there is an increase in the contamination of the food consumed by the cricket, or, perhaps the woodrat droppings become more palatable after the rains.

The heavy infestations of the cricket appears to be one of the factors involved in assuring the complete separation of the adult crickets from one generation to another.

The host-parasite relations between the woodrat and the parasite need further study.

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