

SOME ASPECTS OF THE BIOLOGY OF

STEPHANOFILARIA STILESI

CHITWOOD IN CATTLE

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PREFACE

This research project was selected upon the suggestion of Dr. D. E. Howell, and encouragement of Dr. C. P. Hibler. It was decided that even though the problem was of a veterinary entomology and parasitology nature it would benefit me as a U. S. Navy medical entomologist, because of the valuable experience I would gain in areas of study closely related to my military entomology specialty.

I wish to express my gratitude to my major adviser, Dr. D. E. Howell for his guidance and encouragement throughout this research program and in preparation of this paper. Appreciation and sincere thanks are extended to Dr. E. D. Besch and Dr. R. D. Eikenbary for their support during this research project and for their valuable suggestions and criticisms of this thesis.

I also wish to express my thanks to Dr. T. E. Thedford for his assistance with herd examinations and to Ralph Crane owner of Ralphs Packing Company, Perkins, Oklahoma, and especially to Mr. E. H. Boyd, Chester Crane and H. S. Horsetrotter whose cooperation made part of this research possible.

I am greatly indebted to the United States Navy for giving me the opportunity to conduct this research.

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CHAPTER I

INTRODUCTION

Interest in Stephanofilaria stilesi Chitwood 1934 has been revived only in the past few years. There was no apparent reason, but following its description practically no research was done on this parasite. Although this filariid is a common parasite of cattle in the United States relatively little information has been accumulated about it. The life cycle was not known until 1964 and there is much to be learned about the biology and host-parasite relationships.

Stephanofilariasis is common in Oklahoma cattle. The readily observed lesions and the availability of infected animals provided a wealth of material and it was decided to initiate an investigation to determine the incidence of the infection in local cattle and the effect of breed, age, sex of cattle and of certain environmental conditions on the life cycle of the parasite.

It is hoped that the information gained during this research project will be of benefit particularly to veterinarians, cattle producers, parasitologists and veterinary entomologists.

CHAPTER II

REVIEW OF THE LITERATURE

Stephanofilaria stilesi Chitwood 1934 is common in North America and is one of four species of Stephanofilaria that are nematode parasites which occur in the skin of cattle (Yamaguti, 1961). The adult stages of these worms cause a circumscribed dermatitis known as stephanofilariasis. The lesions of this disease most often occur along the mid-ventral line of the body, but they also have been reported to occur occasionally on the shoulder and medial canthus of the eye (Hansen, 1964). Illustrations and descriptions of this condition have been made by Dikmans (1934, 1948), Maddy (1955), Smith and Jones (1957), and more recently by Jensen and Mackey (1965).

The other three species of Stephanofilaria that affect cattle are S. dedosi Ihle et Ihle-Landenberg 1933 which occurs in Indonesia and produces lesions on the neck, withers, dewlap, shoulders and around eyes; S. assamensis Pande 1936, found in Assam and other parts of India and causes a chronic dermatitis known as "Humpsore;" and S. kaeli Buckley 1937 from Malaysia produces filarial sores on the lower legs of cattle (Smith and Jones, 1957).

There has been some confusion with the description of S. stilesi, particularly with the description of the microfilaria. Chitwood (1934) described the S. stilesi microfilaria as being 680 microns long. Hibler (1966) found they averaged 52 microns in length. Ivashkin, Timofeyeva,

and Khromova (1952) described them to be 18 microns. Ivashkin, Khromova and Shymtova (1963) state that they found cephalic ornamentation on third stage larvae. According to Hibler (1966), development of this ornamentation occurs in the late fourth stage of development.

S. stilesi is distributed throughout North America and Europe and possibly throughout the world. It is found in most states of the continental United States but is more common in the West and Southwest (Lucker, 1956) (Beckland, 1964). There are also reports of infected cattle from Hawaii (Alicata, 1947), the Soviet Union (Gnedina, 1950), Republic of West Germany (Schulz and Schafer, 1965), and Denmark (Hansen, 1964).

The incidence of S. stilesi in areas where it occurs is not well known. Maddy (1955) estimated between 80 and 90% of the mature beef cattle in the western United States were infected. Hibler (1966), in New Mexico, found lesions on over 97% of the beef cattle he examined from range, irrigated pastures and at abattoirs. He found slightly less than 25% of the cattle in dry lots infected.

Hibler (1966) examined seven different breeds of cattle, apparently of both sexes, and made no comparisons of sex or breed susceptibility or resistance to S. stilesi. The literature on S. stilesi is lacking such information. Hibler (1966), however, did correlate the size of Stephanofilaria lesions with the age of hosts in a study involving 45 Hereford cattle.

In another species, S. assamensis Pande 1936, which is similar to S. stilesi, there is a difference in susceptibility between male and female hosts. The males tend to be more susceptible than the females (Srivastova and Dutt, 1963).

The economic importance of S. stilesi is not understood. It is possible that the hide may be devalued and that the blemishes on live animals would be detrimental if they were show cattle. It also could predispose animals to myiasis-producing flies. However, the general health of the animal is not affected (Lucker, 1956) and the condition should not be of major concern to cattle producers.

There have been some attempts made to treat this disease with drugs. Hansen (1964) found that painting the lesion with "Onychophytex Leo" twice daily for about a week killed the nematode. "Onychophytex Leo" was the trade name and the ingredients were unidentified. He followed the "Onychophytex" treatment with the application of zinc chloride to promote healing. Schulz and Schafer (1965) had partial success within a six week period by local treatment of the lesions with 2-3% trichlorophen.

The horn fly, Haematobia irritans (Linnaeus), has been frequently observed associated with S. stilesi lesions. This close association prompted Dikmans (1934) to propose the horn fly as a possible intermediate host. Research in the United States and the Soviet Union confirmed the horn fly as an intermediate host. Ivashkin, Khromova and Shymteva (1963) isolated larvae from the European horn fly, Lyperosia titillans (Bezzi), which were identical to those found in the skin lesions of cattle. Hibler (1964) reported similar findings in H. irritans.

Hibler (1966) demonstrated the life cycle of S. stilesi and confirmed the horn fly as the intermediate host. He made some interesting observations on the host-parasite relationship of S. stilesi and the horn fly, based on Morgan's (1964) findings that environmental tempera-

ture affected the habits of the horn fly on cattle. Hibler (1966) concluded that environmental temperature was an important factor in dissemination of the parasite by the fly.

Hibler (1966) found 20% of the wild female flies infected with S. stilesi larvae in New Mexico in the early summer and fall. During July and August, he noted an almost total absence of infected flies. The warmer temperatures, in his opinion, were detrimental to the development of the larvae in the fly.

CHAPTER III

METHODS AND MATERIALS

Determination of Incidence in Cattle

Cattle were examined in southwest and north central Oklahoma on pastures and ranges, and in abattoirs from August, 1966, through November, 1967. The incidence, appearance and history of stephanofilariasis were determined. The live animals were held in squeeze chutes and the mid-ventral area of the body examined visually and by palpation. Dead animals were examined immediately after slaughter and prior to the removal of the skin. The age, sex and breed of each animal was recorded when it was examined.

Lesions were removed from animals weekly or twice weekly during the periods from August, 1966, until the last week in November, 1966, and from the first week in March, 1967, until the last week in November, 1967. The lesions were taken to the laboratory where they were measured, the excess skin trimmed away (Figure 1), and then lacerated in a crisscross pattern with a sharp knife (Figures 2 and 3). They were then placed skin side down on a plastic screen (Figure 4) in a Baerman funnel (Figure 5) that was filled with warm physiological saline. The funnel was placed in an incubator at 38 C for four hours. After incubation, about 50 cc of fluid were withdrawn from the bottom of the funnel and examined for filariids. The numbers and stages of development were recorded.

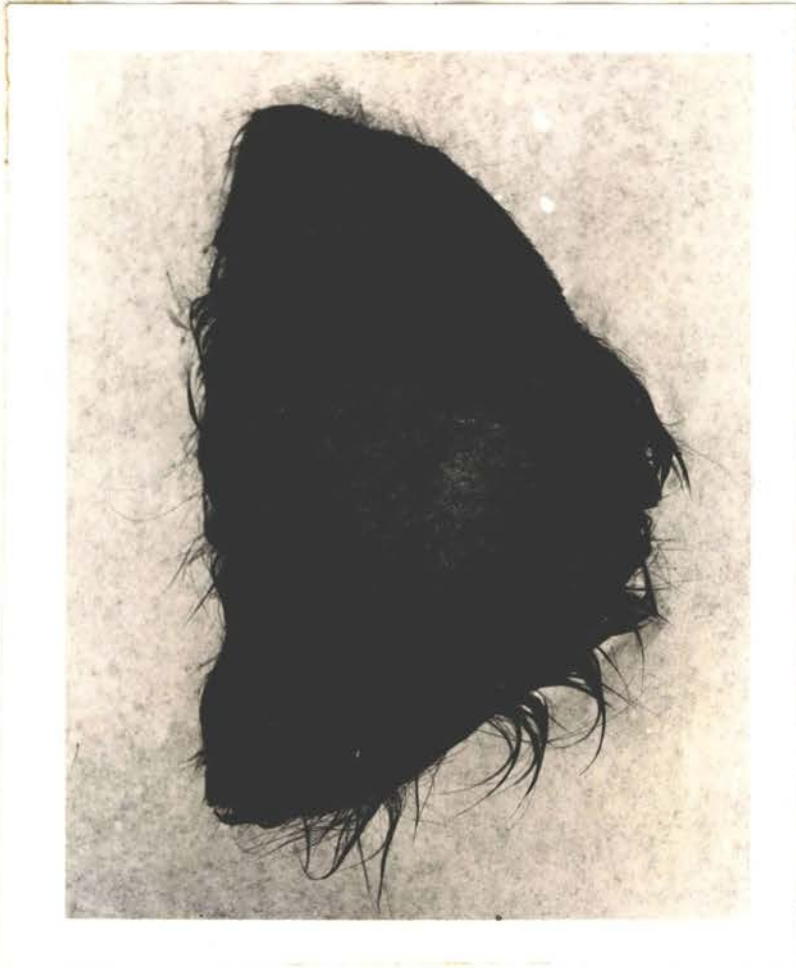


Figure 1. Stephanofilaria stilesi Lesion from a
Yearling Angus Heifer



Figure 2. Method of Cutting Lesion for Removal of Filarids



Figure 3. Appearance of Lesion After Cutting



Figure 4. Stephanofilaria Lesion Placed Skin Side Down
in Baerman Funnel



Figure 5. Baerman Funnel

Rearing of Adult Horn Flies

Approximately 2,000 horn fly pupae were furnished by the Entomology Research Division, Agricultural Research Service, U. S. Department of Agriculture, Kerrville, Texas, each week as required by this study. Approximately 300 pupae were held in a cylindrical paper pint (ice cream) carton and the adults were allowed to emerge into another pint carton with a plastic screen top that was fastened to the pupa holding cage with masking tape (Figure 6). A small hole was made in the bottom of the upper carton to permit flies to move into it from the pupal container. The hole also gave access to the cage for removal of the flies with an aspirator as needed. The adult holding cages (Figure 7) were kept in a temperature-humidity chamber at 90 F and 60% Relative Humidity. Adults were fed twice a day on a cotton pad soaked with bovine blood. Each 1500 mls of the blood diet contained 4 g of sodium citrate, 3.75 g of mycostatin and 500 mg of chloromycetin. This was a slight modification of the diet recommended by Schmidt et al. (1967).

Infection of Intermediate Host in the Laboratory

Two methods were used to establish an infection of S. stilesi in the laboratory. Flies were fed on lesions which had been removed from cattle within 2 hours prior to the time of feeding. The other method involved the feeding of the flies on the bovine blood diet to which microfilaria had been added. Microfilaria were obtained by macerating gravid adult female worms (usually about 10) in 1-2 ml of physiological saline. The macerated mixture was added to about 10 ml of bovine blood. The blood and microfilaria mixture was pipetted on a small cotton pad 5 mm² and the flies were allowed to feed. A total of 300 flies were fed with either method. The flies were allowed to feed

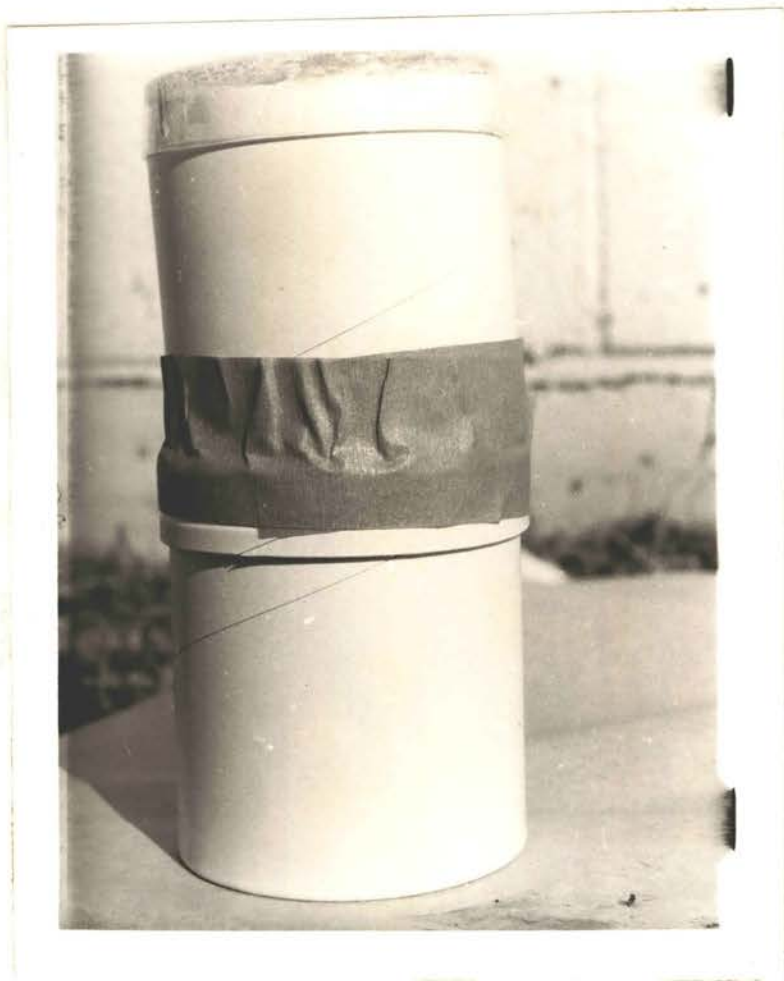


Figure 6. Adult Fly Cage Fastened to Top of Emergence Cage

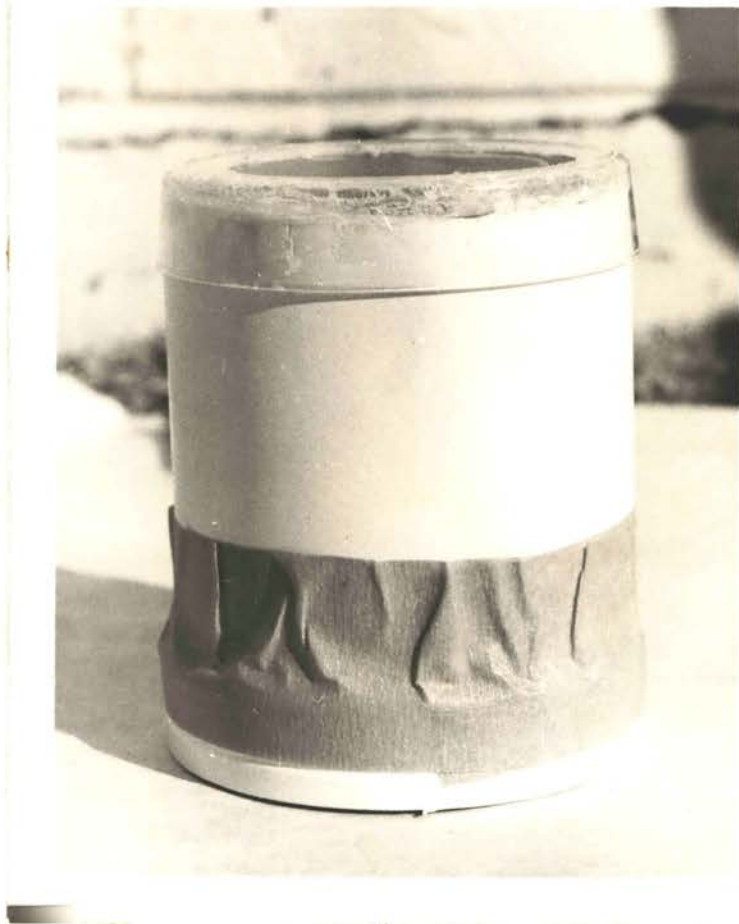


Figure 7. Holding Cage for Flies

1 hour at 50-60% Relative Humidity and 90 F or 50-60% and 70 F, they were then transferred into 3 separate cages with about 100 flies per cage. The cages were then placed in different bioclimatic chambers that were set at temperatures of 50, 70, and 90 F, respectively. In all chambers the humidity ranged from 50-60%.

Evaluation of Intermediate Host Infection

After 48 hours, 20 flies were removed from each cage, dissected and examined for parasites. This procedure was repeated after 72 hours, 7 days, 14 days, and 21 days. These intervals of time were chosen, first, to determine initial infection rate after 48 hours and the subsequent development at the other time intervals and, secondly, to note differences in development between parasites of those flies held at different temperatures.

Temperature and Rainfall Data

Daily extremes of temperature and monthly rainfall amounts for period of study were obtained from the Oklahoma State University weather station.

CHAPTER IV

RESULTS

Incidence in Cattle

Stephanofilariasis was found in 199 of 239 cattle in abattoirs and in 108 of 118 cattle on ranges and pastures in the Stillwater and southwestern Oklahoma areas. All the cattle examined were local cattle and consisted of Angus, Ayrshire, Brahma, Brahma cross, Brown Swiss, Charlaise, Guernsey, Hereford, Hereford-Angus cross, Holstein, Jersey, Mixed (more than two-breed cross), and Shorthorn breeds. The ages of the cattle ranged from less than 1 year to 17 years. Table I shows the incidence by age, sex and breed.

The size, appearance and numbers of lesions present on different breeds and ages of cattle are depicted in Figures 8-12. Figure 8 shows lesions on a yearling Angus heifer. The elongate lesion is 10.5 x 2 cm at the widest point; a second lesion is 1.5 cm in diameter. Figure 9 shows a lesion from a yearling Angus-Hereford cross heifer 6.5 x 2.5 cm. Figure 10 shows two contiguous lesions from a four-year-old Hereford cow, one being 18 x 12.5 cm and the second 6 x 3.5 cm; one separate lesion 5 x 2.5 cm was located on the brisket. Figure 11 shows three lesions ranging in size, from brisket to posterior, 4 cm diameter, 2 cm diameter, and 3 x 1.0 cm from a seven-year-old Angus cow. Figure 12 is a lesion, 10.5 x 6.0 cm from a seven-year-old Hereford bull.

Numbers of lesions found on any one animal ranged from one to

TABLE I.

INCIDENCE OF *S. STILESI* IN 13 DIFFERENT BREEDS ACCORDING TO AGE AND SEX.
EXAMINED IN ABATTOIRS, ON RANGES AND PASTURES.

Breed	Sex	Age and Numbers of Each Positive or Negative for <i>S. Stilesi</i>																					
		1		2		3		4		5		6		7		8		9		10		10+ Yrs.	
		+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Angus	M	5	1	0	-	0	-	1	-	1	-	2	-	8	-	4	-	0	-	1	-	1	-
	F	22	4	2	-	2	-	0	-	0	-	0	-	0	-	0	-	2	-	4	-	0	-
Aryshire	M	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	F	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brahma	M	-	0	-	-	-	1	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-
	F	-	1	-	-	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Brahma Cross	M	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	F	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brown Swiss	M	-	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-
	F	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Charlaise	M	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	F	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Guernsey	M	-	-	1	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	F	-	-	0	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hereford	M	50	10	1	-	1	-	4	-	1	-	1	-	6	-	5	-	-	-	0	-	-	-
	F	74	14	9	-	1	-	2	-	0	-	2	-	0	-	1	-	-	-	1	-	-	-

TABLE I (Continued)

Breed	Sex	Age and Numbers of Each Positive or Negative for <u>S. Stilesi</u>																					
		1		2		3		4		5		6		7		8		9		10		10+ Yrs.	
		+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Hereford	M	3	1	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Angus X	F	14	3	1	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holstein	M	3	1	4	0	1	-	0	0	0	-	0	-	0	-	2	-	-	-	-	-	0	-
	F	1	2	1	2	4	-	4	1	7	1	4	-	9	-	5	-	-	-	-	-	1	-
Jersey	M	1	-	-	-	0	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
	F	0	-	-	-	1	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-
Mixed	M	2	0	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	0	-
	F	6	1	0	-	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	1	-
Shorthorn	M	0	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	F	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
																						TOTAL	341
																						Negative	45
																						Positive	296



Figure 8. Lesions on Yearling Angus Heifer



Figure 9. Lesion on Yearling Angus-Hereford Cross Heifer



Figure 10. Lesions on Four-Year-Old Hereford Cow



Figure 11. Lesions on Seven-Year-Old Holstein Cow



Figure 12. Lesion on Seven-Year-Old Hereford Bull

eight, the average being two and one-half. The sizes varied from 1 cm² (smallest recorded size) to about 300 cm². The largest lesion was observed on a 4-year-old Hereford cow, but the majority of the larger lesions occurred on bulls over 3 years of age. Table II shows a comparison of lesion numbers and sizes with age, sex, and breed of 84 cattle.

Figure 13 represents the times of year the different stages of S. stilesi were found in the host and intermediate host in north-central Oklahoma. The times of occurrence of parasites in cattle and their numbers and stages of development are represented in Figure 14.

Temperature and Rainfall Data

Figure 14 shows the average weekly temperature fluctuations and rainfall amounts from March through November of 1966 and 1967. Relatively high temperatures occurred in July, 1966, including 10 days of 100 F or above. A substantial drop in average temperature from 86 F to 70 F occurred in the week beginning August 22 then increased to 76 F the following week. The average weekly temperature dropped to 70 during the week beginning September 5 and remained 70 F or below thereafter. The first hard freeze occurred on 16 October. Temperatures for summer 1967 were moderate with very few days of 100 F or above. Average temperatures were slightly below those of the same period in the year before.

Evaluation of Intermediate Host Infection in Laboratory

A total of 1500 flies were dissected and examined for parasites. One-hundred flies for each temperature and interval of time. None were found infected.

Stage of Development	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Microfilariae (H)	-----											
1st Stage Larvae (I)			-----									
2nd Stage Larvae (I)			-----									
3rd Stage Larvae (I&H)			-----									
4th Stage Larvae (H)			-----									
Adults (H)	-----											

Figure 13. Numbers and Stages of Development of Parasites in Cattle (H) and Fly (I) and Their Times of Occurrence During Year

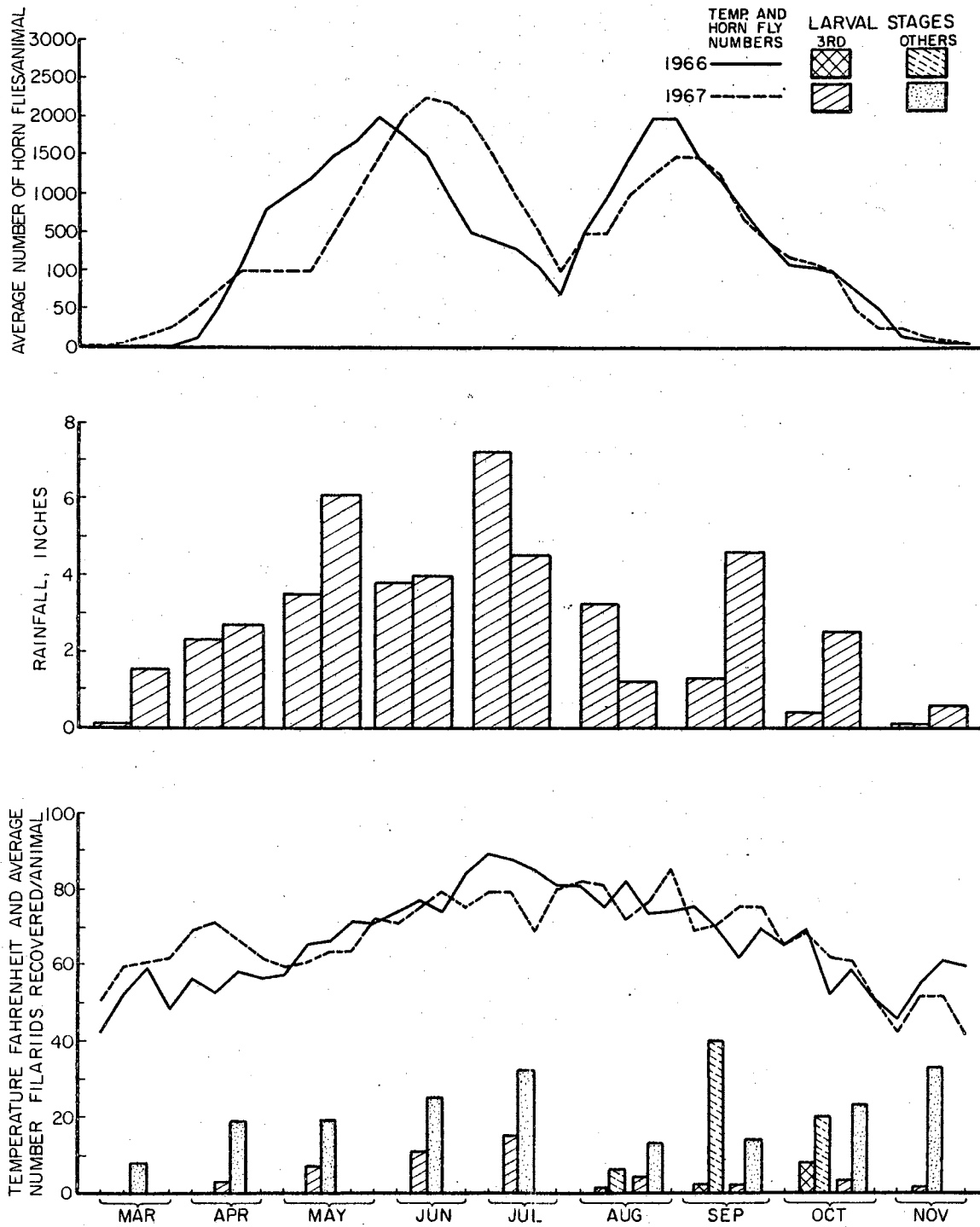


Figure 14. Comparison of Temperature, Rainfall and Fly Populations With Parasite Populations in Cattle for Nine Month Period

CHAPTER V

DISCUSSION

The incidence of S. stilesi in Oklahoma cattle is comparable to that found by Hibler (1966) in New Mexico. However, Hibler (1966) made no distinction between the age, breed, or sex of the cattle except for 45 Herefords examined. He correlated lesion size with age of the animal. He found a much higher percentage of infected cattle on the range than in feedlots and theorized that this was because of the difference in horn fly populations on cattle in each environment. The number of flies on animals being much higher on range and pasture cattle than feedlot cattle. There is no doubt that the fly populations do differ in both situations. But, if the majority of the cattle in a herd are mature animals, according to the interpretation of data collected in this investigation, one would expect to find a much higher incidence of infection than if the majority of the animals were calves. The age of cattle along with environment determines numbers of flies present on each. Horn flies prefer to feed on more mature animals and a herd of calves will have far less flies per animal than a herd of more mature animals, other factors being the same (Morgan, 1964). Most feedlot cattle are young animals, so the ages should also be considered when determining incidence of infection with S. stilesi.

The breed of cattle seems to have little effect on its susceptibility or resistance to S. stilesi with the exception possibly of the

Brahma. Only five pure bred Brahmas were seen during this study--one yearling, three three-year-olds, and one six-year-old. None of these animals had any indication of a lesion. The sample size was too small to substantiate any claim that the Brahma breed was resistant to S. stilesi. It was learned from the manager of the abattoir who cooperated on this research, that to his knowledge he never recalled seeing the sores on any Brahma cattle. Animals that are cross bred with Brahmas are susceptible. Hibler (1966) observed lesions on Brangus and Santa Gertrudis. Brahma crosses were also found infected in this study.

The sexes appeared to be equally affected with the disease but there was a tendency for the older male animals from which filaria infected lesions were removed, to have the larger lesions (See Table II). Bulls tended to have more flies per animal than cows and there was a difference in the thickness of skin from the mid-ventral region, the bulls having the thicker of the two sexes. It is difficult to speculate that either one of these factors might possibly cause the difference in lesion size. All the lesions observed on both sexes, occurred along the mid-ventral line. The reason for this region of the body being affected entirely and not other regions, was not ascertained.

Environmental temperature governs the daily behavior of the horn fly and is probably one of the most important factors in the dissemination of S. stilesi (Hibler, 1966). According to Morgan (1964), horn flies prefer temperatures from 73 F to 80 F. In early morning and on cool, cloudy days, flies can be observed scattered over the back and sides of cattle. When the daily temperatures rise above 80 F, the flies move to the shade areas of the animal's body, usually along the mid-ventral region. Hibler (1966) states that this results in an excellent

TABLE II
 AVERAGE NUMBER AND SIZES OF LESIONS FOR FOUR GROUPS TOTALING 84 CATTLE
 ACCORDING TO AGE AND SEX

Breed	Sample Size	<u>Age Group and Sex</u>							
		3 Years and Under				3 Years and Over			
		<u>Male</u>		<u>Female</u>		<u>Male</u>		<u>Female</u>	
Number of Lesions cm ²	Size of Lesions cm ²	Number of Lesions cm ²	Size of Lesions cm ²	Number of Lesions cm ²	Size of Lesions cm ²	Number of Lesions cm ²	Size of Lesions cm ²	Number of Lesions cm ²	Size of Lesions cm ²
Hereford	40	1.2	8.14	1.9	7.66	2.1	22.67	2.0	45.00
Angus	13	1.2	9.16	2.4	7.70	1.6	101.08	3.0	7.28
Holstein	11	4.0	3.92	2.5	7.5	3.0	17.79	2.0	11.34
Other	20	1.3	6.31	1.6	8.87	---	---	3.0	9.52
Avg. for all		1.9	6.88	2.1	7.94	2.3	47.18	2.5	18.28

host-parasite-vector relationship since the flies prefer to feed on the lesions located in the mid-ventral region.

The close association of flies with the filarial lesions on extremely hot days would indicate that the rate of infection of horn flies and transmission to cattle is at its highest peak at this time. The opposite appears to be true. Hibler (1966) found fewer infected flies in the months of July and August in New Mexico. He reasoned that the higher temperatures were detrimental to the development of the larval parasite in the fly and even though more flies were feeding on lesions and becoming infected, fewer were found infected because the larval filariae never developed.

Temperature and rainfall can have pronounced effects on other factors which can be correlated with numbers of infected flies present. Figure 14 shows a correlation of temperature and rainfall with horn fly populations and the average number of third stage Stephanofilaria larvae recovered from lesions using the Baerman technique. The small numbers of third stage larvae in August indicates that there is a reduction in transmission rate during this time. Whether this is due to the reduced fly population or whether for the reason Hibler (1966) gave for finding fewer infected flies, is not clear.

The fact that Hibler (1966) did find some infected flies during the months of July and August indicates that some filaria larvae did develop in the flies if they became infected. This brings up the question: Are the flies feeding and not becoming infected for some reason if exposed to microfilariae, or are there fewer infected flies exposed because the fly population is reduced and therefore fewer flies to become infected?

Attempts to infect flies in climate controlled cabinets, temperature 70 F and 90 F and humidity 50-60%, in the laboratory were unsuccessful when they were fed on fresh lesions and blood-soaked cotton pads containing microfilariae. The flies were observed to feed in all instances and viable microfilariae were recovered from the lesions after the flies had fed, which would indicate the flies had the opportunity to become infected but for some reason did not.

The results of this study indicate that rainfall, fly populations and possibly other factors as well as temperature are very important to the host-parasite-vector relationship of cattle, S. stilesi, and H. irritans. Further research is needed to determine just what factors or combination of factors are responsible for the difference in transmission rates during a complete fly season.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Stephanofilariasis was found in 199 of 239 cattle in abattoirs and in 131 of 135 cattle on ranges and pastures in the Stillwater and southwestern Oklahoma areas. The cattle examined were native to Oklahoma and consisted of 10 breeds and three cross breeds. The ages of the cattle ranged from less than one year to 17 years.

The numbers of lesions found on cattle ranged from one to eight and the sizes varied from about 1 cm² to about 300 cm². Lesions were found on all breeds examined except Brahma (only five Brahma cattle were examined) and were equally common on male and female animals. The majority of the larger lesions were found on male animals over 3 years of age.

Environmental temperature and rainfall were correlated with horn fly populations and numbers per animal of third stage filariids recovered from lesions by the Baerman method.

All breeds except for possibly the Brahma, and both sexes appear to be equally affected with the disease and the disease is more prevalent on mature animals.

Relationships were demonstrated between the environmental temperatures, rainfall, horn fly populations and average numbers of third stage larvae recovered from individual animals. The results indicate that one or a combination of these factors affect the rate of trans-

mission of S. stilesi from the definitive host to the intermediate host and from the intermediate host to the definitive host.

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VITA

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