BEHAVIORAL OBSERVATIONS OF FED AND UNFED STAGES OF THE LONE STAR TICK, *AMBLYOMMA AMERICANUM* (LINNEAUS), IN RESPONSE TO VARIOUS ENVIRONMENTAL PARAMETERS

By

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PREFACE

This thesis summarizes a series of field studies on the behavior of the lone star tick [*Amblyomma americanum* (Linneaus)] in the Cookson Hills State Game Refuge, Cherokee County, Oklahoma. An attempt has been made to correlate lone star tick behavior with various environmental factors. Ticks appeared to respond primarily to the effects of temperature and relative humidity.

Sincere thanks go to my major advisor, Dr. J. A. Hair, for his patience, assistance, and guidance in completing this research.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure		Page

CHAPTER I

INTRODUCTION

The Cookson Hills State Game Refuge in Cherokee County, Oklahoma is comprised of 14,000 acres of natural terrain designated in 1951 primarily for the use of propagating the white-tailed deer, *Odocoileus virginianus* (Boddaert). Along with the planned increase in deer production came the unwanted increase of one of the most important pests of the region, the lone star tick, *Amblyomma americanum* (Linneaus). In recent years the lone star tick population has reached sufficiently high levels to account for up to 60% mortality of the annual fawn crop. In addition to wildlife losses ticks contribute to weight losses in livestock and annoyance to man due to their bloodsucking habits. Equally important, some diseases of man including Rocky Mountain spotted fever, Tularemia, and tick paralysis are transmitted by this species. Because of these facts the lone star tick has become known as a noxious pest and has undoubtedly hindered the economic development of eastern Oklahoma to the fullest of its potential. Without fear of attack by this pest many vacationers would consider this part of Oklahoma a recreational paradise and tourism could be the source of considerable economic gain for an area which might otherwise remain underdeveloped.

The purpose of this study was to observe the behavior of fed and unfed stages of the lone star tick in response to temperature, humidity, photoperiod, and habitat type. Engorged larvae and nymphs were released at different times during their active period to determine the effect of season on their molting times. Post-molt observations of the engorged nymphs included activity and attachment rate to a host. Engorged larvae were released in two habitat types in order to compare longevity of the resulting nymphs.

The literature yielded very little information on engorged female ticks in the field. The purpose of the replete female study was to observe ovipositional behavior, egg hatching, and post-hatch behavior of resulting larval lone star ticks.

The unfed adult and nymph studies were designed to correlate temperature, photoperiod and humidity with vertical migration and activity of the ticks. Studies on unfed larvae were made to correlate environmental conditions with vertical migration and diurnal movement. Semtner (1972), Hair and Howell (1970), and others (Drummond, 1967; Lancaster, 1957; Sonenshine, et al., 1966) have shown that nymphal lone star ticks have two activity peaks in a single season, whereas adults have only a single peak per season. In order to develop effective control procedures one must know as much as possible about the natural history of the lone star tick. Important areas of study include its life cycle under field conditions, and its response to environmental factors. These biological studies can be of great use in developing control strategies. Other authors have found that clearing areas of woody vegetation was extremely detrimental to all stages of the lone star tick (Hoch, et al., 1971; Clymer, 1969). These data when analyzed with corresponding biological information could lead to an effective means of reducing tick populations to an acceptable level.

CHAPTER II

LITERATURE REVIEW

The historical record of ticks' harassment of man dates back a considerable period of time. Arthur (1965) cites a photograph of head fragments of a "hyaena-like" animal from an Egyptian tomb which he feels shows evidence of the presence of ticks. The contents of the tomb date about 1500 B.C.

Early reports of ticks include those by Aristotle (355 B.C.) and Pliny (77 A.D.). Aristotle stated in his Historia Animalium that "ticks are generated from couch grass".

The economic importance of ticks was brought to light by Smith and Kilbourne (1893) who discovered that the causal organism of Texas cattle fever, *Babesia bigemina* (Smith and Kilbourne) was transmitted by the tick, *Boophilus annulatus* (Say). Since that time numerous pathological organisms have been shown to be vectored by ticks (Sacktor, et al., 1948). Among them are Rocky Mountain spotted fever, relapsing fever, Tularemia, anaplasmosis, American Q fever and Bullis fever.

The first tick identified in the United States was the lone star tick, *A. americanum*. It is the most abundant tick species in Arkansas and Oklahoma (Eddy, 1940; Lancaster and MacMillan, 1955). In addition, the lone star tick has been reported to be the most abundant species in other eastern and southern states (Hooker, et al., 1912; Calhoun, 1954; Drummond, 1967). The lone star tick acquired its name from the prominent white spot at the posterior angle of the female's scutum. The male is smaller and has a few irregular white markings and two horse-shoe shaped areas at the posterior-dorsal margin of the abdomen. *A. americanum* has four stages in its life cycle: (1) egg; (2) larva or "seed tick"; (3) nymph or "yearling tick"; and (4) the adult (Lancaster, 1957, 1970). Adult ticks can be positively identified by the presence of a genital aperture, which is lacking in the larval and nymphal stages (Furman and Catts, 1970). Nymphal and larval lone star ticks are unmarked and, like the adults, have a reddish brown color.

Life History and Seasonal Cycle of the Lone Star Tick

The lone star tick is described as a "three-host" tick which means that each stage requires a blood meal before molting to the next stage or egg deposition as in adult females. The engorged larvae and nymphs drop from their host animal for molting. The adults mate on the host from which the fully engorged female drops to the ground and lays several thousand eggs. After egg deposition the female dies.

Each active stage of the lone star tick climbs up on vegetation while awaiting a host animal. If unsuccessful in securing a host during their first season of activity the larvae will die, while nymphs and adults may overwinter and seek a blood meal the next season.

Longevity of the lone star tick is dependent upon environmental factors. Feldman-Muhsam (1947) observed that both larvae and nymphs of *Hyalomma savignyi* Gerv. are much more sensitive to relative humidity than temperature. This same author noted that their longevity at low humidity is short as compared with that at high humidity. In contrast, Semtner, et al. (1971b), indicated that temperature is the primary factor that affects longevity of _A. americanum_ under field conditions. Semtner, et al. (1971b) further stated that habitats characterized by certain types of vegetation may show drastic climatic differences and may allow as much as three times the longevity afforded by a less favorable habitat.

Numerous authors (Lees, 1946, 1947, 1948b; Browning, 1954; Belozerov and Seravin, 1960; Edney, 1966; Noble-Nesbitt, 1969; Hafez, et al., 1970) have reported on the ability of various arthropods to prolong their life span by absorbing moisture from their environment. Sauer and Hair (1971) indicated that the lone star tick also possesses the ability to absorb moisture from atmospheres of high relative humidity. High numbers of the lone star tick are distributed throughout the Ozark mountain region, an area characterized by dense underbrush. This area provides a microclimate in which the humidity remains high throughout the year (Semtner, et al., 1971b).

Activity of the lone star tick varies according to the seasonal weather conditions (Sonenshine, et al., 1966; Semtner, et al., 1971b, 1973a,c). This variation becomes evident when comparing the annual activity of this acarine as reported by different authors (Brennan, 1945; Lancaster, 1955, 1957; Tugwell and Lancaster, 1963; Drummond, 1967; and Semtner, 1971b).

The seasonal cycle of the lone star tick in eastern Oklahoma was reported by Hair and Howell (1970) to be as follows: (1) Larval activity starts in mid-June, peaks in late July or early August and subsides in early November; (2) Nymphal activity begins in late February or early March, peaks in late June and again in early

September and subsides in early October; and (3) Adult activity begins in late February or early March, peaks about mid-June and subsides in late July or early August.

Sweatman (1967) states that longevity of replete Rhipicephalus sanguineus (Latreille) females is temperature dependent and is shortened significantly by a low relative humidity between 20 and 30°C. Lancaster and MacMillan (1955) and Arthur (1951), working with A. americanum and Ixodes hexagonus Leach, respectively, observed an inverse relationship between relative humidity and the pre-oviposition period. These observations with I. hexagonus and A. americanum show the opposite trend to that seen in a study presented by Sweatman (1967) where low relative humidities shortened the pre-oviposition period of R. sanguineus.

Hosts

The lone star tick has a wide host range and all active stages readily attack man (Bishopp and Trembley, 1945; Brennan, 1945; Tugwell and Lancaster, 1962; Clymer, et al., 1970b). Bequaert (1946) and Lancaster (1957) reported that all stages are frequently found on the same host. Clymer, et al. (1970b) stated that the larger, more wide ranging animals were most heavily parasitized by the lone star tick. The data indicates that the lone star tick is not host specific and that host size and habits may be the governing factors involved in the host-parasite relationship for this species.

Ticks have been shown to move towards an increase in concentration of CO_2 to an area near the release point, regardless of whether the source of CO_2 is artificial or natural (Garcia, 1962, 1965, 1969; Wilson, et al., 1972). Smittle, et al. (1967) used radioisotopes to find that the lone star tick tended to move toward shaded areas. Apparently the shaded areas in their test plots served as cover for wildlife, which created a scent that attracted the ticks as was reported by Smith, et al. (1946). Preference of the lone star tick for wooded areas is thought to be due to the need for high relative humidity which is present in these areas (Lancaster and MacMillan, 1955; Lancaster, 1957).

Distribution

Eddy (1940) found that the lone star tick was distributed throughout much of southern and eastern Oklahoma. Bishopp and Trembley (1945) stated that the lone star tick was found in large numbers in wooded areas, particularly where underbrush was dense, such as along river bottoms, in prairie areas, and in canebreaks. Calhoun and Alford (1955), while studying Tularemia in lone star ticks in Arkansas, noted that on a 160 acre farm the highest concentration was found in a small wooded area measuring approximately 75 square yards. Concentration of cattle within this area for shade as well as the humid conditions along a wet weather creek bed provided excellent habitat for the large population of ticks found there. Lancaster (1957) found that brushy pastures were more heavily infested with _A. americanum_ than open, improved pastures. The typical tick habitat in Arkansas is brushy or timbered areas, which are generally unsuited for cultivation. Lancaster (1957) found that nearly 70% of the lone star ticks taken in his survey were from brush as compared to only 1.5% taken from open pasture. Sonenshine, et al. (1966) showed that the lone star tick was distributed more or less uniformly in 4 woody vegetative types in Virginia. However, the combined grasses-andherbs habitat type had significantly lower adult and nymphal densities when compared to the woody type.

Several factors may cause the irregular distribution of ticks. Milne (1943), in northern England, suggested that because I. ricinus larvae from one egg mass are concentrated within a small area, hundreds may attach to a host at the same time and will replete and drop off at about the same time. Nymphs, therefore, should also tend to occur in localized areas which will be relatively large as compared to those of larvae. Milne (1946) found that I. ricinus populations were lower in sheep pens due to lack of vegetative cover. Vegetation was too sparse and the ground too dry to support ticks.

MacLeod (1936) stated that the problems underlying the local distribution of ticks are simplified by the habit of feeding that ticks have evolved. Being dependent on the will of their host for dispersal, ticks exercise no selection relative to their habitat conditions. The factors which determine the suitability of a habitat are primarily edaphic: the nature of the soil, presence or absence of a humus-forming layer, and vegetative type.

The availability of suitable hosts and relative humidity are 2 major factors limiting the distribution of many ticks. Lancaster and MacMillan (1955) demonstrated that a lack of moisture often limited survival of the lone star tick. In a tick-host survey by Clymer (1970b) in eastern Oklahoma, the leading hosts of A. americanum were white-tailed deer and cattle. McMahan (1966) found that the white-tailed deer in the Kerr wildlife management area, Texas, were generally observed to feed in particular sites. These sites appeared to correlate with proximity to overstory cover. Deer are found most abundantly along the forest margins where the heaviest desirable cover and the greatest amount of available food in the form of low-growing shrubs and bushes is found (Bartlett, 1938).

CHAPTER III

METHODS AND MATERIALS

Study Area

The Cookson Hills State Game Refuge, located in southeastern Cherokee and southwestern Adair counties, Oklahoma, was selected as the study area. This area was chosen because of its number of ticks and its availability for isolated studies. This area is known for its deer population which has been affected severely by the lone star tick.

Unfed Adult Study, 1972

Four separate upland oak-hickory habitat types (all habitat types used are those classified by Semtner, et al., 1971b) were selected as release sites. Ticks released at each of these sites were confined by constructing an arena of 20 cm. steel garden edging material formed into 75 cm. diameter rings. The bottom edge of the arena was buried 3-5 cm in the soil. Around the top edge of the arena was placed a band of "Stikem Special[R]" which served to prevent the escape of ticks. At each release site a 1.2 meter high net wire enclosure was erected to prevent disturbance by large mammals. Because the enclosures were constructed at the time of the first release and subsequent releases were planned, ample area was allowed within the enclosures to prevent unnecessary disturbance when making observations.

Releases of ticks were made at monthly intervals from April to

August at a rate of 50 ticks/arena (25 females, 25 males). Each release was repeated 4 times, i.e., once in each of the study areas. In order to make observations on individual ticks, 4 pair/arena were marked with different colors as described by Wilson, et al. (1972). All ticks used for release in the study area were field collected in the manner outlined by Hair, et al. (1972), counted and marked, and immediately released into the prepared site.

Observations were made at weekly intervals and included location and orientation of marked and unmarked ticks in the arenas, temperature, photoperiod and humidity. Initial observations included the number of ticks on vegetation and leaf litter before disturbance and the total number of ticks after disturbance. "Disturbance" consisted of exhaling into the arena 10 times and counting the ticks as they moved over the leaf litter. Ticks were recorded as "active" if they were either visible on the vegetation before disturbance or if they appeared on the litter after disturbance.

Unfed Nymph Study, 1972

Nymphal lone star ticks were studied in the same manner as the adults in that 4 upland oak-hickory habitat types were constructed in the same manner as previously described and ticks were collected and released as described. Nymphs were released at a rate of 100/arena and were released at monthly intervals from April to July.

Unfed Larva Study, 1972

Four similar upland persimmon-ecotone habitat types were chosen as release sites. Arenas and enclosures were constructed as previously described. Releases were made at monthly intervals from 31 March to 14 August and were replicated 4 times, or once in each of the study areas.

Larvae were obtained by allowing laboratory fed females to oviposit. Ticks which were to be used in this study were selected and released immediately after completion of hatching was evident. Each release consisted of a mass of several thousand larvae placed into an arena in each of the 4 different areas.

Observations included temperature, humidity, position of ticks within the arena, period between release and upward movement, and longevity. Initial observations were made at daily intervals and subsequent observations on a weekly basis after the larvae had ascended the vegetation within the arena.

Engorged Female Study, 1972

Replete female lone star ticks were collected from live-trapped, white-tailed deer. They were then released immediately into the same type arena as described earlier. Releases were made once a month from April-July in 4 different locations in the same habitat type (upland oak-hickory). Each release consisted of 5 engorged females/arena in each of the four locations. The females were released at random within the arenas and allowed a one-week acclimation period. After this period the ticks were located and their position marked with 3.2 mm dowel pins.

Observations were initially made three times each week but were reduced to once a week (the reasons will be discussed later in this paper). Observations included: (1) preovipositional behavior, orientation, and site selected for oviposition; (2) preoviposition time in days; (3) hatching time of eggs and (4) larval activity.

Engorged Nymph Study, 1972

Flat nymphs were field collected around carbon dioxide traps (Wilson, et al., 1972) at monthly intervals from April-September and engorged on rabbits which had not been used previously for tick rearing.

Rather than using the arenas described in previous studies, it was decided that the screenwire cage (Semtner, et al., 1973e) would be more appropriate for this experiment. In order to determine molting time of the engorged ticks it was necessary to examine the leaf litter closely. Therefore, the arena type enclosure with a band of "Stikem Special^{R}" was determined to be unsatisfactory. Cages were placed in an upland oak-hickory habitat and engorged nymphs were released at a rate of 300/cage. Three cages were used for each of the releases.

Observations were made at weekly intervals until the ticks were near molting, at which time daily observations were made. The ticks were considered to have completed molting when all of the first 50 ticks observed had molted.

Engorged Larva Study, 1972

Laboratory reared larvae were allowed to engorge on rabbits which had not been used previously for rearing purposes. The engorged larvae were then released in two habitat types (upland oak-hickory and meadow) into four metal rims per habitat type, at the rate of 1000 ticks/rim. The metal rims were the larger, outside rim which was part of the screen wire cage used in the engorged nymph study and described by Semtner, et al. (1973c). This rim was placed in the selected habitat type and then driven into the ground about 2.5 cm. or until it was firmly planted. As in the arenas used in other studies, a band of "Stiken Special^{R}" was placed around the top, inner edge to prevent the escape of the resulting nymphal lone star ticks.

Molting time was determined by counting the first 50 ticks observed in each rim at three day intervals. When molting began, observations were increased to daily intervals and reduced to three day intervals when no unmolted ticks could be found. Cessation of activity was determined by observing each of the releases until no activity could be observed.

Unfed Adult Study, 1973

There were some procedure changes made in the 1973 study as compared to the 1972 study. They were: (1) utilization of two habitat types (upland oak-hickory and meadow); (2) six replicates in each habitat type; and (3) one release consisting of 25 pairs of adult ticks per replicate per habitat type. There were two upland oak-hickory sites, each with three arenas, and two meadow habitat sites, again, each with three arenas.

Adult ticks were captured using the method of Wilson, et al. (1972) and were released into the fenced enclosures early in the active season. One release consisting of 25 pairs of adult lone star ticks/arena was made on 31 March 1973 and observed until activity had ceased. "Activity" was determined by the same method described in the earlier adult tick study.

Unfed Nymph Study, 1973

This study was carried out in the same manner as the preceding study, i.e., upland oak-hickory and meadow habitat types, six replicates per habitat, and one release which was observed until activity ceased. Ticks were released into the arenas in the enclosed study sites at a rate of 1000/arena. Nymphal lone star ticks were field captured around carbon dioxide traps and released within a few hours to minimize any effects of handling. The same observations were made and recorded as with the 1972 flat nymph study.

Flat Larva Study, 1973

This study was designed to observe the behavior of larval lone star ticks in four different habitat types (meadow, upland oak-hickory, persimmon-ecotone, bottomland oak-hickory). Masses of larvae were located in all habitat types, except the meadow, and were observed four times during each 24 hour period for five days. Because no larval masses could be found in the meadow habitat a group was located in an upland oak-hickory habitat and relocated to the meadow.

Care was taken while making observations not to disturb the masses of seed ticks. Observations included type of plant on which the ticks were located, time of observation, orientation in relation to the sun, changes in size of mass, and vertical movement of mass.

Engorged Nymph Study, 1973

Field collected nymphs were engorged on rabbits and released into meadow and upland oak-hickory habitat types at a rate of 300 ticks/cage. There were three cages per habitat type per release. The cages were constructed as described by Semtner, et al. (1973a).

Observations were made at bi-weekly intervals until it became evident molting was soon to begin, at which time daily observations were made. Ticks were recorded as completely molted when all of the first 50 counted were molted. Observations included molting time, and periods of inactivity and activity.

Engorged Larva Study, 1973

Replete female lone star ticks were collected from various wild and domesticated hosts and were allowed to oviposit. The resulting larvae were then engorged on rabbits and released into upland oak-hickory and meadow habitats. As in the 1972 larva study, metal rims with a band of "Stikem Special[R]" were used to retain the ticks. Three rims were placed in each habitat from 30 March to 4 September 1973 and engorged larval ticks were released at a rate of 1000 per rim.

Observations included molting time, initiation and cessation of activity, and comparison of behavior in the two habitat types. The ticks were considered completely molted when all of the first 50 counted were molted.

Climatological Data

Temperature and relative humidity of the various habitat types was recorded continuously by Bendix model 594 hygro-thermographs (Bendix Corp., Frieze Instrument Division, Baltimore, Maryland 21201) on seven-day charts. These hygro-thermographs were housed in standard field weather station structures which were located in four habitat types (persimmon-ecotone, meadow, bottomland, and upland oak-hickory). Mean temperatures and humidities for the various study areas were derived from these instruments.

Precipitation amounts were derived by averaging the data recorded for Sallisaw, Tenkiller Dam, Stilwell, and Tahlequah weather stations (U. S. Department of Commerce, National Climatic Center, Federal Building, Asheville, N.C. 28801).

Additional temperature data was collected using a YSI Telethermometer (Yellow Springs Instrument Co., Inc., Yellow Springs, Ohio 45387) with a multichannel probe system. This enabled the researcher to record temperatures at various levels in each habitat type (Hoch, et al., 1971).

CHAPTER IV

RESULTS AND DISCUSSION

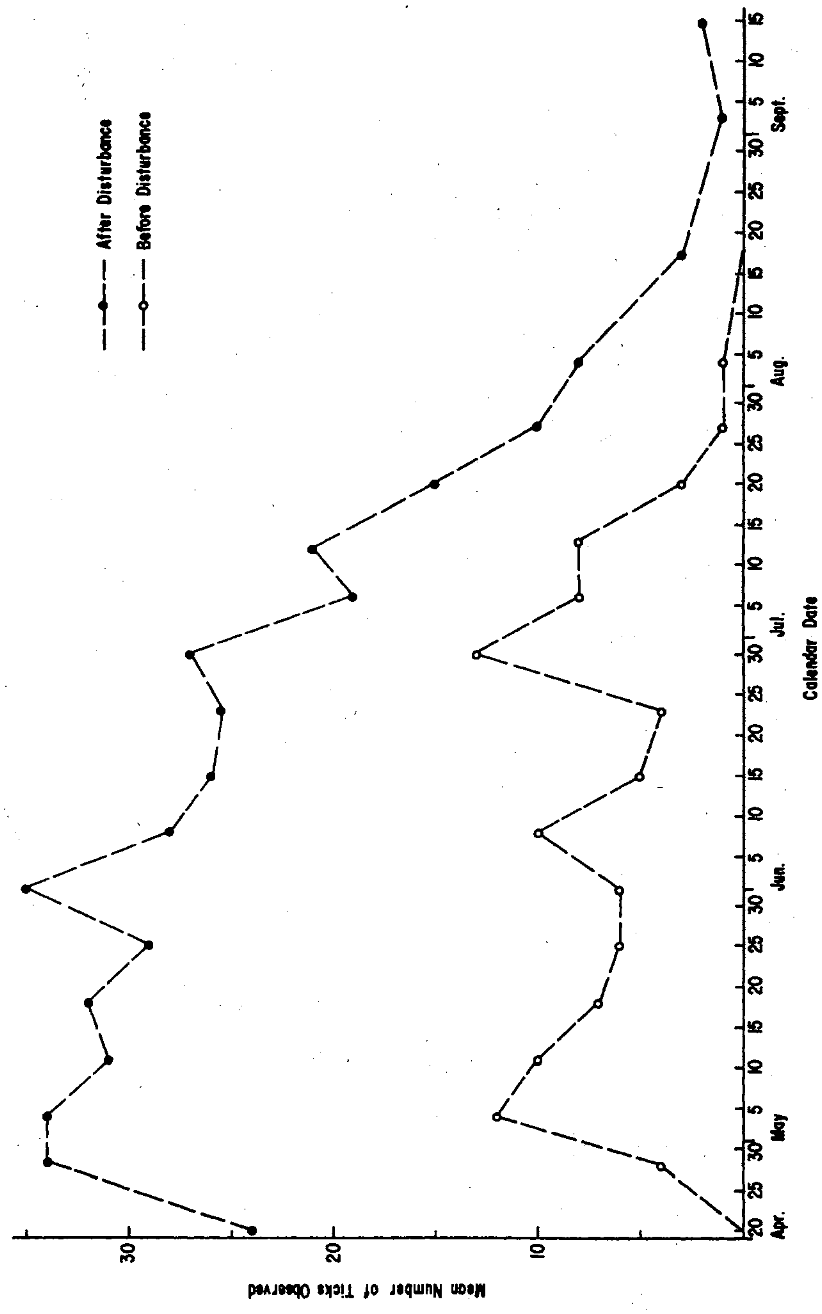
Effect of Climatic Factors on Unfed Adult Ticks During 1972 and 1973

Behavior in Upland Oak-Hickory; 1972 and 1973

Of the climatic parameters measured during 1972 and 1973 the combination of temperature and humidity had the most noticeable effect on adult lone star tick behavior in the upland oak-hickory habitat. High temperatures in combination with lower average humidities during 1972 and 1973 caused a gradual decline in total numbers of ticks active from April to September (Figures 1, 2; Appendix 13, 14). Those ticks in the upland oak-hickory habitat which were active late in the summer at a time of decreasing temperature and increasing humidity probably became quiescent because of decreasing photoperiod.

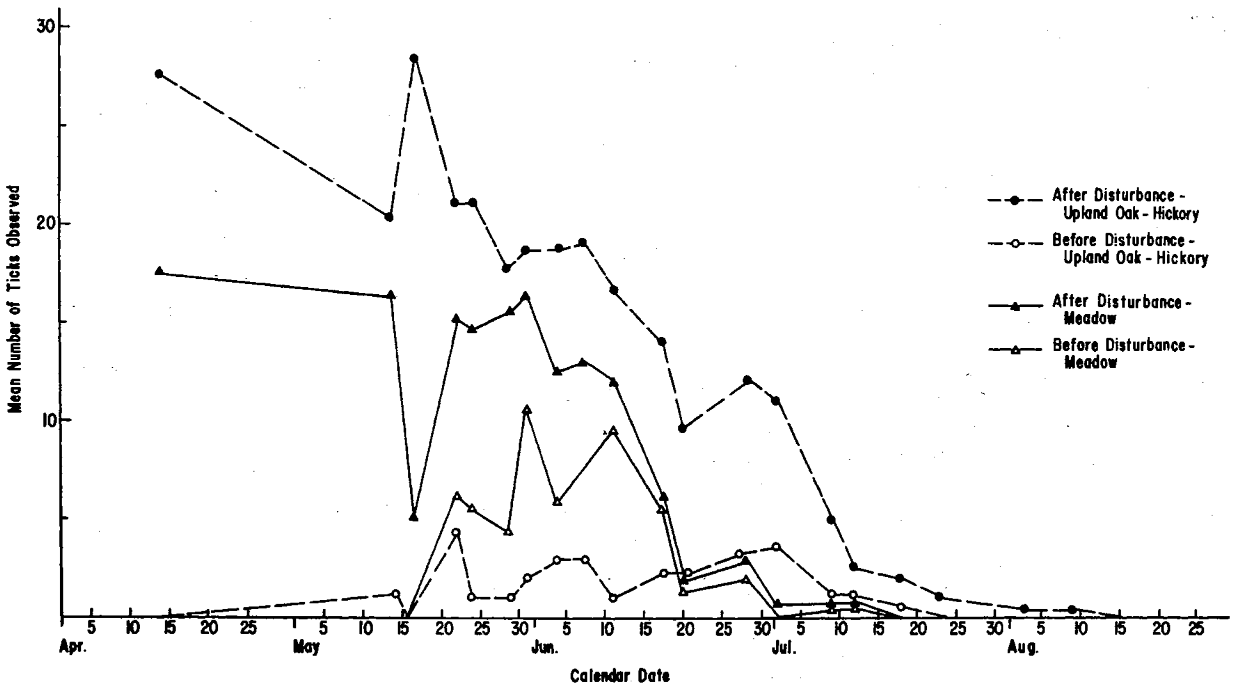
All field collected adult ticks released in the upland oak-hickory habitat type between April and August 1972 and in March 1973 exhibited similar activity patterns (Figures 1, 2; Table VI, Appendix). The activity patterns for the first release during 1972 are graphically represented in Figure 1 and behavioral patterns for the March 1973 release is depicted in Figure 2. The mean number of ticks observed on the vegetation and leaf litter before disturbance reached peaks in early May and late June in 1972 (Figure 1), whereas, the peak activity

Figure 1. Activity of Adult Lone Star Ticks in an Upland Oak-Hickory Habitat in Cherokee County, Oklahoma, During 1972



After Disturbance
Before Disturbance
Mean Number of Ticks Observed
10
20
30
Calendar Date
Apr.
May
Jun.
Jul.
Aug.
Sept.

Figure 2. Activity of Adult Lone Star Ticks in Two Habitat Types in Cherokee County, Oklahoma, During 1973


Mean Number of Ticks Observed
30
20
10
5 10 15 20 25 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25
Apr.
May
Jun.
Jul.
Aug.
Calendar Date
After Disturbance - Upland Oak - Hickory
Before Disturbance - Upland Oak - Hickory
After Disturbance - Meadow
Before Disturbance - Meadow

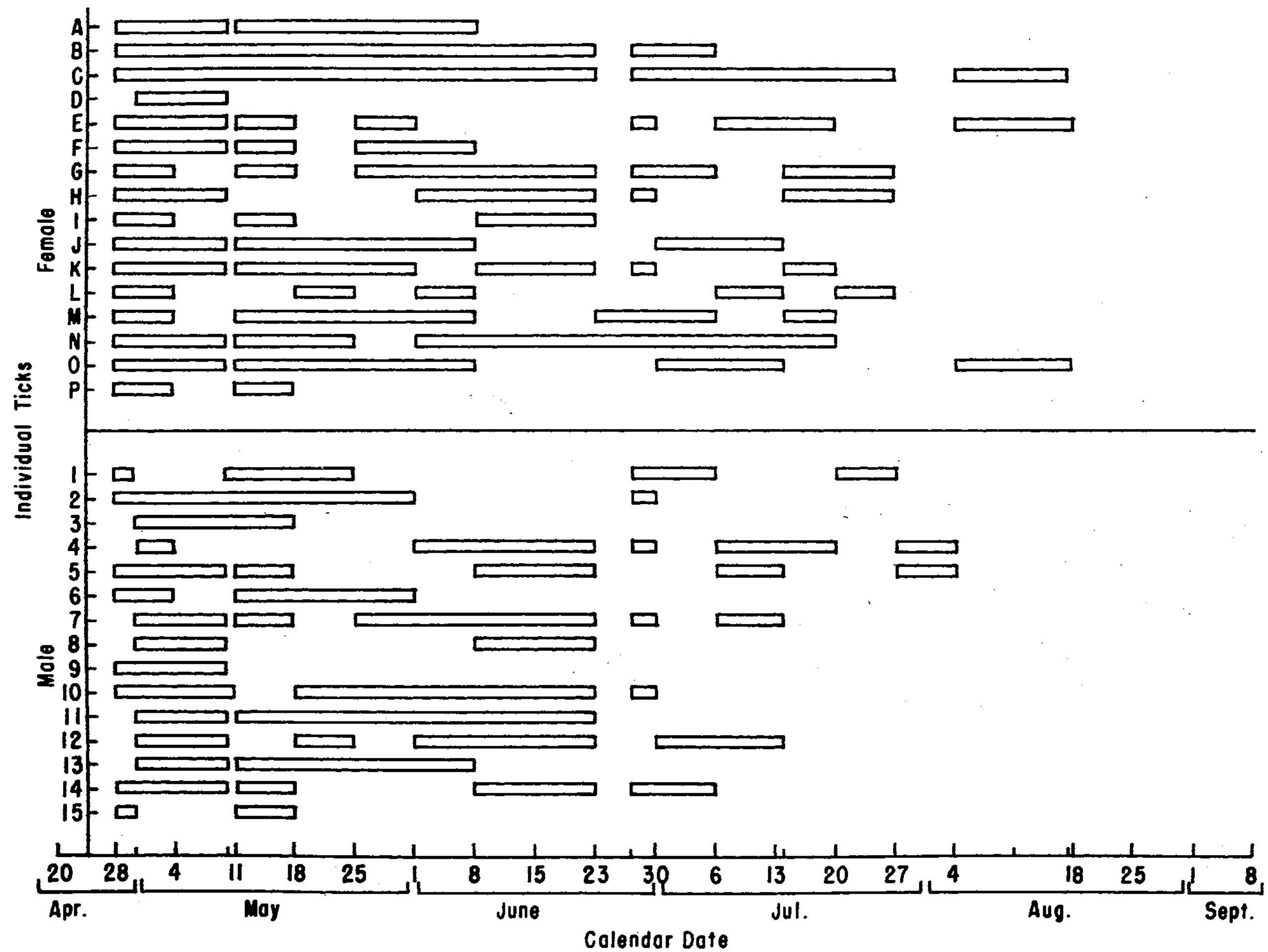
occurred on 22 May and 2 July during 1973 (Figure 2).

It appears that the most important parameter affecting tick behavior in the upland oak-hickory habitat during 1972 and 1973 was temperature. The mean daily temperature in this habitat during 1972 rose from approximately 15°C in late April to about 25°C in late June (Figure 13, Appendix) and temperatures were generally higher during 1973 than in 1972 (Figure 15, Appendix). Adult activity during 1973 had ceased by 15 August despite the higher average relative humidities recorded during the 1973 study period (Figure 2 and 14, Appendix), whereas, activity was recorded as late as 15 September during the 1972 study. When compared to the 1973 studies the 1972 observation period was characterized by lower average temperatures and lower average temperatures and lower average relative humidities (Figure 13 and 14, Appendix). The humidity in the oak-hickory habitat during 1972 decreased from about 88% in mid-April to 52% in mid-August (Figure 13, Appendix), whereas, during 1973 the humidity readings ranged from about 83% on 1 May to 70% on 15 August (Figure 14, Appendix). The humidities recorded during 1973 were generally higher than those recorded in 1972. This was due to increased amounts of rainfall experienced during the period from April through September. Tables IV and V (Appendix) show that nearly twice as much precipitation was recorded during 1973 as compared to the 1972 study period. It is possible that adult lone star ticks began descending the vegetation during the 1972 and 1973 study periods in response to an upper temperature limit in a manner similar to that noted for other tick species. Larval _Ixodes ricinus_ L. were shown to be negatively geotatic between 14 and 24°C and positively geotactic above and below that temperature range (MacLeod, 1935). Further work is necessary to determine the temperature range within which lone star ticks ascend or descend vegetation.

Although the role of relative humidity on tick behavior has received little study, its effect on total body water content is important (Sauer and Hair, 1971; Lees and Milne, 1951). The gradual decline in total number of ticks observed from May to September during 1972 and 1973 (Figures 1 and 2) could have been an indication that the ticks were requiring longer periods of time in the leaf litter near the soil in order to replenish their dwindling body water reserves or that mortality was occurring as a result of inadequate food reserves. Sauer and Hair (1971) have shown that A. americanum has the ability to absorb water from atmospheres with greater than 85% relative humidity. The effect of relative humidity in prolonging activity of adult lone star ticks in the oak hickory habitat during 1972 and 1973 was probably lessened by the higher temperatures encountered during June, July, and August of those years. Because the ability of ticks to utilize atmospheric moisture in regulating body water content is hampered by high temperatures (Lees and Milne 1951; MacLeod 1935) one might expect that ticks in this study had to spend more time in the leaf litter, because water regulation was more difficult. This is reflected by the declining numbers of adult ticks observed after disturbance in the upland oak-hickory habitat during 1972 and 1973 (Figures 1 and 2). This belief is supported further by Figure 3, which indicates that marked individual adult ticks exhibited shorter periods of activity during July and August than during April - June.

Adult ticks during 1972 and 1973 began ascending vegetation in late April and began descending leaf litter in early July. The majority of

Figure 3. Activity of Individual Ticks Observed in an Upland Oak-Hickory Habitat Type in Cherokee County, Oklahoma, During 1972


Individual Ticks
Female
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Male
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
20
28
4
11
18
25
1
8
15
23
30
6
13
20
27
4
18
25
1
8
Apr.
May
June
Jul.
Aug.
Sept.
Calendar Date

ticks ascended when photoperiod exceeded 14 hours of daylight. The total number of ticks observed to be active during 1972 and 1973 did not appear to be correlated to photoperiod because of a decline in total number of ticks observed after disturbance during a period of increasing day length in May and June of both years (Figures 1 and 2; Appendix 13, 14). This indicated that rather than day length, some factor or factors such as temperature and relative humidity were probably regulating tick activity. Photoperiod may be important from the standpoint of preventing ticks from engorging late in the season at a time which would expose them to unfavorable temperatures during oviposition. Balashov (1972) states that photoperiod may be important in controlling diapause in ticks and that without diapause, or some form of quiescent stage, seasonal control of the life cycle will be poor and partially superimposed successive generations are possible.

Behavior in the Meadow, 1973

In summarizing the data presented in Figure 14 (Appendix) we note that the relative humidity curves plotted for both habitat types were relatively constant during the period from April to mid-August. Temperature curves during the same period showed the characteristic rising trend during the latter part of the summer. The lack of the characteristic inverse temperature:relative humidity ratio, as detected by hygrothermograph during 1973 was probably caused by increased amounts of precipitation from April through September (Figure 14 and Table IV, Appendix). Other workers (Semtner, et al., 1971b) have demonstrated that the meadow habitat is subject to extremes in relative humidity and temperature on a daily and seasonal basis. In contrast, the upland oak-hickory habitat showed less variation in daily temperatures and generally lower average humidities than the meadow during 1973 (Figure 14, Appendix). The meadow habitat generally had high night-time relative humidities (98-99% RH) and low daytime relative humidities (30-35% RH). The average relative humidity, as measured by hygro-thermographs, from April to mid-August was 80% in the meadow and 70% in the oak-hickory habitat. It was noted that temperatures recorded at 15.2 cm above the soil surface in the meadow habitat exceeded 35°C after 4 July and that temperatures at the soil surface were generally 4-5°C above those recorded at 15.2 cm (Figure 14, Appendix). In contrast, temperatures measured at the soil level in the upland oak-hickory habitat were always lower than those measured at 15.2 cm. during 1973. It appears that a temperature gradient in the meadow was created by the lack of overstory vegetation with the high temperatures at the plant bases and lower temperatures at the plant tips. A similar phenomenon was reported by Semtner, et al. (1971b).

Activity in the meadow habitat during 1973 produced a similar curve to that of the oak-hickory habitat but the total numbers of ticks observed never equaled that of the forest (Figure 2). The figure indicates that unlike the oak-hickory habitat which showed two to three peaks in numbers of ticks ascending the vegetation, the adult ticks in the meadow habitat peaked on the vegetation in early to mid-June and then declined rapidly until mid-July at which time no active ticks could be observed. Possible explanations for this behavior in the meadow might be (1) that the ticks had entered a quiescent stage in the litter or (2) that adverse environmental conditions caused high mortality and that the ticks observed during the latter part of the study represented those which had not yet succumbed. Of the two explanations it is believed that the latter is more reasonable. Figure 2 indicates that although the total number of active ticks in the meadow habitat never equalled the total number active in the oak-hickory habitat, the number of ticks observed on the vegetation in the meadow was considerably higher than that recorded for the oak-hickory during the period from mid-May to late June. Figure 2 also shows that from mid-June until mid-July, when tick activity in the meadow was decreasing, most of the ticks observed to be active in this habitat were observed on the vegetation. The inverse temperature gradient which was described earlier probably created a humidity gradient in the meadow habitat with the higher humidities at the vegetation tips and lower humidities at the plant bases. This occurrence was also noted by Semtner, et al. (1971b). With this in mind it appears that the adult lone star ticks in the meadow, which were observed at the vegetation tips from mid-June to mid-July during 1973, were possibly selecting a zone which was characterized by lower temperatures and higher humidities than could be found at the plant bases. The explanation of the high mortality experienced by the ticks in the meadow during 1973 may be that the effect of high temperatures amplified the effect of low humidities. MacLeod (1935) noted in working with I. ricinus that as temperature increased, the effect of humidity in prolonging the survival period steadily diminished. It appears that the cause of the consistently higher number of adult ticks observed on vegetation in the meadow than in the upland oak-hickory habitat was the inverted temperature and humidity gradients which were forcing the ticks to the vegetation tips.

In the 1973 study, as in 1972, activity of adult ticks in the upland oak-hickory habitat was initiated when approximately 14 hours of daylength had been reached and was declining when daylength had fallen to about the same period after a high of 14 hours and 45 minutes (Figure 14, Appendix). The ticks in the meadow habitat (Figure 2) began ascending the vegetation during mid-May which corresponds with about 14 hours daylength (Figure 14, Appendix) but the numbers observed on the vegetation began decreasing in early to mid-June. Daylength was still increasing at this time and it appears probable that the declining population in the meadow habitat during 1973 was due to mortality as was indicated by Semtner (1972).

In comparing the 16 May observations on Figure 2 and the corresponding observations on Figure 14 (Appendix) one notices the significant decrease in total numbers of active ticks observed in the meadow and the contrasting increase in total number active in the upland oak-hickory habitat type. Climatic conditions recorded at the time of observation indicate a sharp drop in temperatures at all levels measured and a corresponding low relative humidity. Other data recorded at this time reveal that although this particular day was sunny there was considerable wind at the time of observation. The site chosen as a representative upland oak-hickory habitat bordered the western edge of the meadow habitat and was generally protected from the prevailing winds. It is possible that the adult ticks in the meadow habitat were exhibiting a wind avoidance response, whereas, the ticks in the forest habitat were protected from the wind and were exhibiting a response to other environmental conditions. Lees and Milne (1951) reported that adult I. ricinus exhibited a highly significant avoidance response to wind and in fact was more concerned with escaping the effects of wind than the effects of sun.

Behavior of Individual Adult Ticks During 1972

The active period referred to in Figure 3 was defined by Lees and Milne (1951) as the interval between the first and last appearance on the vegetation. This definition was expanded to include not only those ticks observed on the vegetation but those which responded to the investigator's breath and behaved as though actively seeking a host.

A high percentage of the marked ticks were observed to be active at least once on observations subsequent to their release with 6% of the males and none of the females unaccounted for (Table I).

The duration of active life is normally considerable shorter than the length of the whole life span. From Table I it can be seen that males were active 36 days on the average as compared to a mean of 52 days that the females were active. These data are similar to those recorded by Lees and Milne (1951) who observed that a maximum activity of 54 days was achieved by a female I. ricinus.

Successive active phases of individuals seldom exhibited any noticeable regularity as can be seen in Figure 3. The quiescent phase was usually shorter (9.4 days for males and females) than the active phases (13.1 days for males and 15.1 days for females). This is opposite the behavior of I. ricinus individuals which were noted to have longer quiescent phases than active phases (Lees and Milne, 1951). These workers noted that the mean duration of activity was shorter for females than for males which agrees with the information gathered in this study.

Figure 3 suggests that it is unusual for a tick to remain active throughout its known life span. Where a series of active phases are

TABLE I

SUMMARY OF OBSERVATIONS ON INDIVIDUAL TICKS IN AN UPLAND OAK-HICKORY HABITAT TYPE IN CHEROKEE COUNTY, OKLAHOMA, 1972

	Male	Female
% of Marked Ticks Observed at Least Once	94	100
Mean Days of Activity	36.2	51.8
Range Days of Activity	10-68	11-99
Mean Days in Single Period of Uninterrupted Activity	13.1	15.1
Mean Days Between Periods of Activity	9.4	9.4
Mean Number of Active Phases	2.9	3.3
% Active One Time Only	13.3	6.25

separated by periods of inactivity, it may be that the pattern of activity was regulated by tick body water content. Lees (1946) noted that one day in an environment above the critical equilibrium humidity was sufficient for unfed I. ricinus to regain any lost water. Shih, et al. (1973) observed that unfed adult lone star ticks regained a maximum amount of weight, interpreted as regained body water, within 2 to 4 days after introduction of the organisms to the high humidities used in their laboratory studies. In laboratory experiments using A. americanum as the test animal a water loss equal to about 10-15% of the original weight was needed to elicit a significant response to the high humidities in a humidity gradient chamber (Hair, unpublished data)[1]. Lees and Milne (1951) found that I. ricinus adults sought high humidities after a 12% loss in weight (water). Assuming that this behavior in response to relative humidity serves as a "safety valve" that prevents excessive dessication during prolonged periods of activity, one might speculate that the regulation of the up and down movements enabled the lone star ticks in the 1972 study to remain at the tips for more total days than would otherwise be possible. Even if this were not the case this type of behavior may have served simply to spread the active phases over a longer period of time. This may, in turn, have had some value by increasing the probability of locating a suitable host. As was discussed earlier, it appeared that the ability of lone star tick adults to utilize humidities above the critical equilibrium humidity was modified chiefly by temperature. This is reflected in Figures 1, 2, and 3 which show that the total number of ticks observed

[1]Unpublished data. J. A. Hair. Associate Professor, Department of Entomology, Oklahoma State University, Stillwater, 1974.

during 1972 and 1973 decreased steadily from May to September.

An apparent cessation of activity of adult ticks and subsequent reactivation was observed on June 23 (Figure 3). Although no quantitative data was recorded concerning this point, it was observed that ticks seemed to be sluggish and less responsive when observed during a rainstorm. It was raining at the time of observation on 23 June (Table IV, Appendix) and it is believed this is reflected in Figure 3.

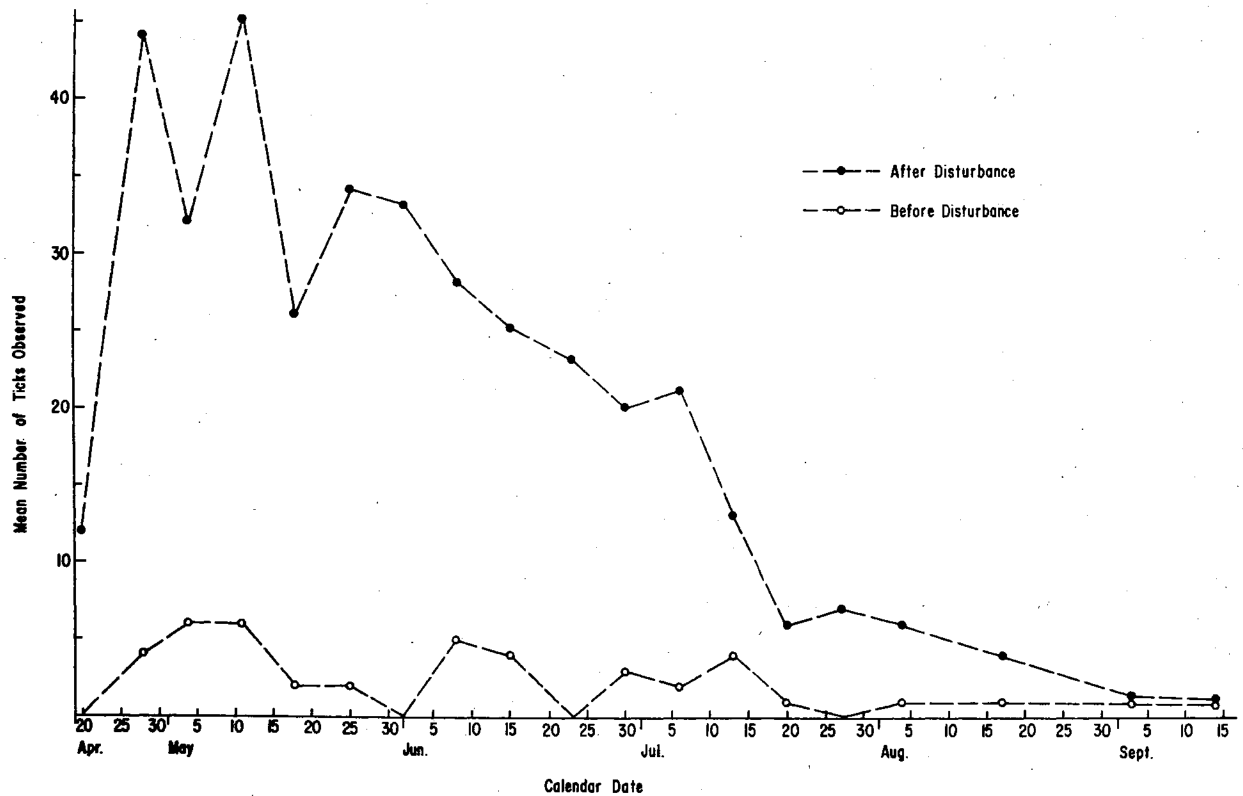
Effect of Climatic Factors on Unfed Nymphal Ticks During 1972 and 1973

The unfed nymphal studies carried out in 1972 were similar to the adult studies of that year in that (1) activity had a similar peak and rate of decline and (2) all releases showed similar activity patterns (Table VII, Appendix). Since the activity curve for each of the releases was similar, all were averaged together and are presented in Figure 4. Climatic data collected during the study period is presented in Tables IV and V (Appendix) and Figures 13 and 14 (Appendix).

Behavior in the Upland Oak-Hickory Habitat, 1972 and 1973

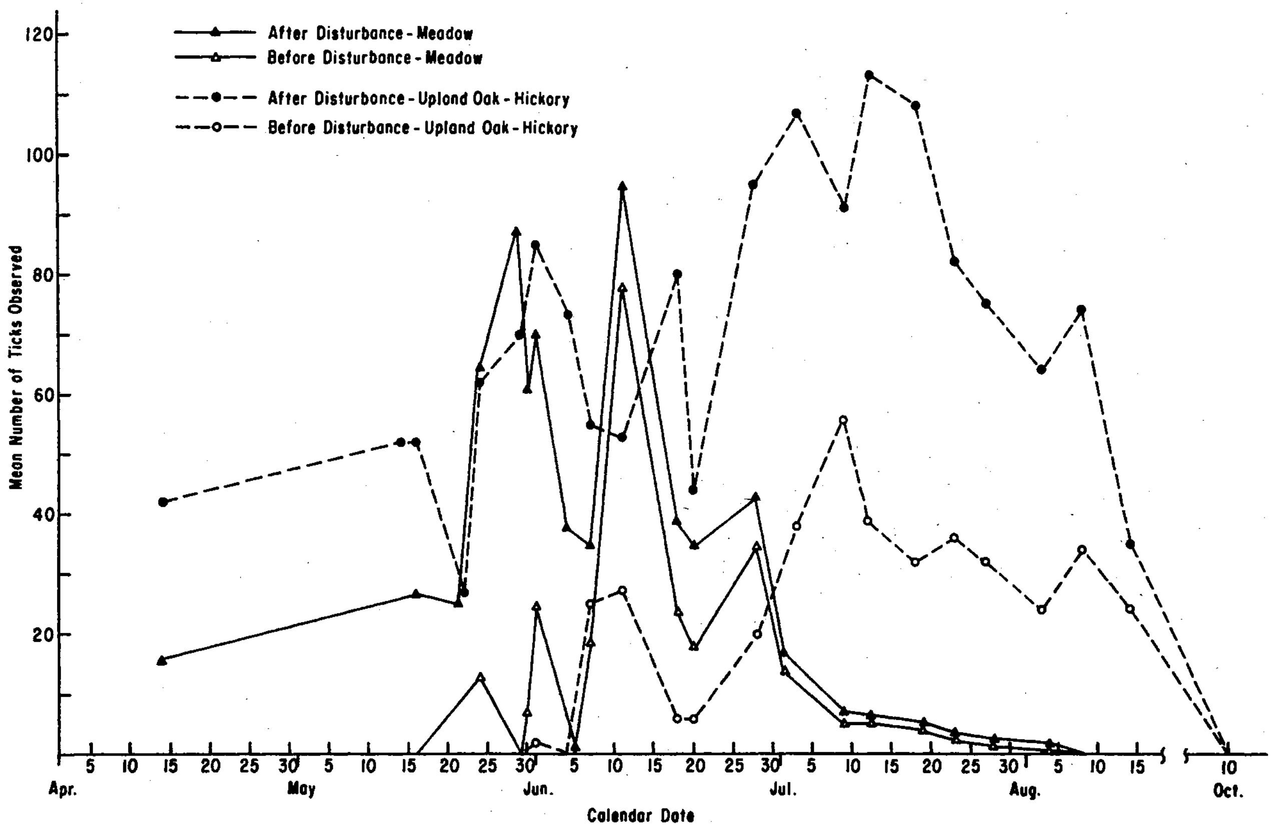
Nymphal behavior in 1972 closely resembled the adult activity curves with a peak in total numbers of active ticks observed on 10 May followed by a decline in activity until mid-September when the last observation was made (Fig. 4). Figure 5 shows that ticks released in 1973 exhibited a totally different pattern of behavior. In 1972 (Figure 4) the nymphs became active in late April, reached peak activity a few weeks later, and declined steadily after mid-May. In contrast,

Figure 4. Activity of Nymphal Lone Star Ticks in an Upland Oak-Hickory Habitat Type in the Cookson Hills Game Refuge, Oklahoma, During 1972



After Disturbance
Before Disturbance
Mean Number of Ticks Observed
Calendar Date
Apr.
May
Jun.
Jul.
Aug.
Sept.

Figure 5. Activity of Nymphal Lone Star Ticks in Two Habitat Types in the Cookson Hills Game Refuge, Oklahoma, During 1972



After Disturbance - Meadow
Before Disturbance - Meadow
After Disturbance - Upland Oak - Hickory
Before Disturbance - Upland Oak - Hickory
120
100
80
60
40
20
Mean Number of Ticks Observed
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 10
Apr.
May
Jun.
Jul.
Aug.
Oct.
Calendar Date

nymphs observed in 1973 became active in mid-April, reached moderate numbers in June, and peaked in mid-July after which there was a rapid decline in activity.

These contrasting activity patterns may be explained by referring to relative humidities recorded in the oak-hickory habitat and by the rainfall data recorded for the Cookson area. In comparing the climatic data for the two years we see that the average daily relative humidity for the upland oak-hickory habitat was usually higher in 1973 (Figures 13 and 14, Appendix). The higher relative humidity was probably created by the higher amounts of rainfall during the 1973 study period (Table V, Appendix). In comparing Tables IV and V (Appendix) one can see that from April through September 1973 nearly 1000 mm of precipitation was recorded while during the same period in 1972 only 530 mm were recorded.

Although it is doubtful that data collected by means of hygrothermographs can be used with confidence to characterize the microhabitat of the lone star tick, it can be useful in the comparison of gross atmospheric measurements. When comparing the 1972 temperature data (Figure 13, Appendix) with temperatures recorded by hygrothermographs in 1973 (C. D. Patrick)[2] it was noted that the average daily temperature was within a few degrees on any given date. This was the case in both the upland oak-hickory and the meadow habitat types. From Figure 15 (Appendix) the mean temperature at two levels (soil and 15.2 cm) in the oak-hickory habitat was calculated to be 23°C and 28°C, respectively, during the 1972 study period. This compares to 26°C and

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[2]Personal communication. C. D. Patrick, graduate research assistant, Department of Entomology, Oklahoma State University, Stillwater, 1974.

29°C at the soil level and 15.2 cm during the second season of study.

One can speculate that relative humidity was more important than temperature in determining survival time of nymphal lone star ticks during the 1972 and 1973 study periods. This was noted to be true for nymphal _Hyalomma savignyi_. Feldman-Muhsam (1947) also noted that length of life of nymphal _H. savignyi_ increased directly with humidity and inversely with the temperature.

The explanation for the mid-July peak of nymphs in 1973 may be that the average relative humidity was higher during this period (74% RH in 1973 as compared to 69% RH in 1972). These higher humidities were associated with the increased precipitation falling from April to September during the 1973 study period (Table V, Appendix). Figure 15 (Appendix) reveals that the temperature at the soil level in the oak-hickory habitat during 1973 reached 30°C and above in mid- to late July. This corresponded to a decline in activity of the ticks in the oak-hickory habitat. Nymphal lone star ticks during the 1973 study perhaps were responding in a manner similar to that reported for larval _I. ricinus_ (MacLeod, 1935). With humidity limitations removed the nymphal lone star ticks were positively phototactic at temperatures above about 30°C.

Semtner (1972) characterized the upland oak-hickory habitat type as having moderate leaf litter cover and light undergrowth. Because the atmospheric humidities were higher in 1973 than in 1972 (Figures 13 and 14, Appendix) due to increased precipitation (Tables IV and V, Appendix), one may assume that the effect of leaf litter in preventing loss of soil moisture (Billings, 1970) created a microhabitat with substantially higher relative humidities. These added moisture reserves may have enabled the nymphal ticks to continue seeking a host until high temperatures became a limiting factor.

In comparing Figures 4 and 5 one notices that a larger number of ticks were observed before disturbance in 1973 than in 1972. Specifically, 36% of the nymphal lone star ticks judged to be "active" in the 1973 study were observed on leaf litter, twigs, etc., before disturbance. In comparison, 11% of the "active" ticks in the 1972 study were observed before disturbance. This may be accounted for by the increased relative humidities experienced during the 1973 study.

If photoperiod played a role in determining the activity cycle of nymphal lone star ticks during the 1972 and 1973 study periods it was not a major one. This is evidenced by the fact that the study populations in 1972 were decreasing while photoperiod was increasing; conversely, the 1973 tick activity was declining at a time when days were rapidly becoming shorter (Figure 4, 5 and 14, 15 Appendix). Photoperiod may exert an influence on those ticks still active late in the season when temperatures have fallen and humidities have normally increased. The function of this mechanism would be to prevent engorgement at a time that would make molting to the next stage improbable before winter conditions arose. Semtner, et al. (1973c) postulates that success in maintaining the tick's life cycle is dependent on the engorged nymphs molting into adults prior to inactivation by cool October temperatures. Should the nymph fail to molt, then its chances of overwintering in Oklahoma appear to be reduced.

Behavior in the Meadow Habitat, 1973

An interesting contrast in the 1973 nymphal study is found by comparing the ticks in the meadow and upland oak-hickory habitat types (Figure 5). From the figure we can see that the period of activity in the meadow (115 days) was considerably shorter than that in the oak-hickory habitat (178 days). Activity had ceased in the meadow by early August in 1973. In constrast, favorable environmental conditions allowed activity in the forest habitat until early October. In addition, an average of 45% of the ticks observed in the meadow were on the vegetation before disturbance (Figure 5). It is important to realize that as of early June, 90% or greater of the ticks observed to be active in the meadow were observed on the vegetation before disturbance.

Although the average daily humidities in the meadow were higher than those in the upland oak-hickory habitat during 1973 (Figure 14, Appendix) they apparently were not effective in prolonging the ticks' period of activity. The reason they were not effective is probably that the lack of overstory in the open meadow habitat allowed the temperatures at the soil level and at 15.2 cm to reach intolerable extremes (Hoch, et al., 1971).

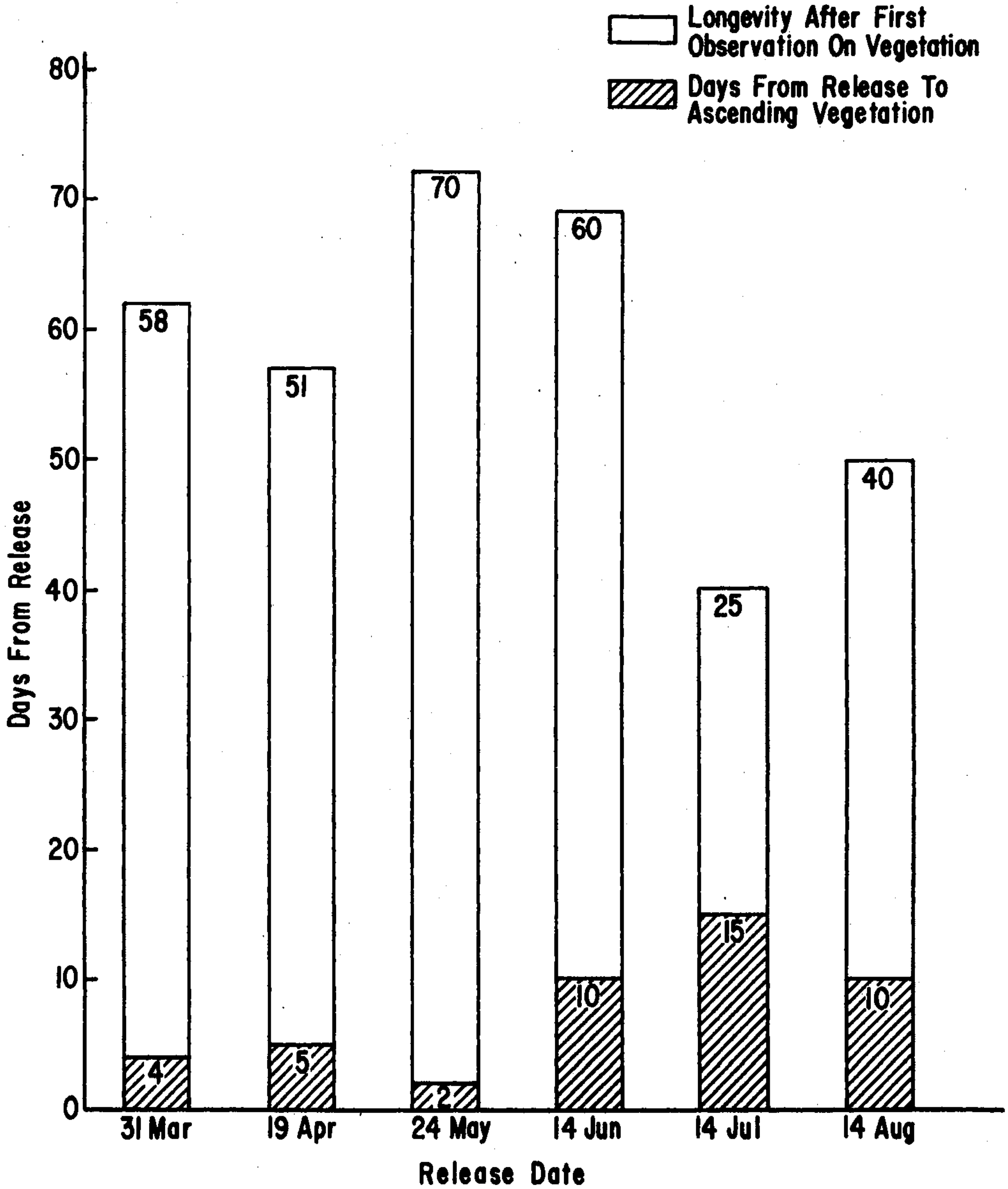
The probable explanation for the high percentage of ticks observed on the vegetation before disturbance in the meadow (45%) as compared to the upland oak-hickory habitat (36%) is made evident by Figure 14 (Appendix). As was explained in the unfed adult studies the temperature gradient inversion observed in the meadow created a humidity gradient with the high humidities at the plant tips. This is illustrated in Figure 5 which indicated that by mid-June 90% or greater of the ticks observed in the meadow were on the vegetation. The temperature at the soil level in the meadow at this time was greater than 40°C.

Although no data was recorded it was the researcher's personal observation that the ticks observed during the latter stages of the 1973 study in the meadow represented most of the extant population. Those ticks observed late in the 1973 season in the oak-hickory habitat did not represent the total population of viable ticks. Sluggish, but live, ticks could be found in the forest habitat when searching the leaf litter. Increased mortality in the meadow habitat has been recorded by other researchers (Semtner, et al., 1971b).

Effect of Climatic Factors on Unfed Larval Ticks During 1972 and 1973

Newly hatched larval lone star ticks placed in a persimmon-ecotone habitat type in March, April, and May ascended the vegetation within 2-5 days (Figure 6). Those larvae released during June, July, and August ascended the vegetation in 10-15 days. According to Balashov (1972) most newly hatched larvae remain inactive for some time and do not leave the hatching site. Observations on larval behavior in the field are scant and factors that stimulate larvae to climb the vegetation are unclear. One possible explanation for the delay in ascending the vegetation exhibited by the last three larval releases is that the low humidities of the late summer in some way hampered the rate of post-hatch development. Feldman-Muhsam (1947) noted that larval _H. savignyi_ were much more sensitive to humidity than to temperature. Wilkinson (1953), working with _Boophilus microplus_ (Canestrini), sought an answer to the question of whether larvae ascend the vegetation because of a positive phototaxis or a negative geotaxis. He concluded that light appeared to be the dominant factor causing the ascent of the

Figure 6. Results of Observations on Larval Lone Star Ticks in a Persimmon-Ecotone Habitat Type in Eastern Oklahoma During 1972.


Longevity After First Observation On Vegetation
Days From Release To Ascending Vegetation
Days From Release
80
70
60
50
40
30
20
10
0
58
51
70
60
25
40
4
5
2
10
15
10
31 Mar
19 Apr
24 May
14 Jun
14 Jul
14 Aug
Release Date

larvae. Krijgsman (1937) found in laboratory experiments with _B. annulatus_ (Say) (believed by some authors to be _B. microplus_) that larvae introduced into tubes gradually became more photopositive four days after emergence and were attracted to light. In view of the above information it is possible that larval lone star ticks during 1972 (Figure 6) ascended the vegetation due to a positive phototactic response. A similar phototactic response was reported for larval _I. ricinus_ by MacLeod (1935). The positive response to light exhibited by _A. americanum_ larvae was acquired gradually during the post-hatch development phase. The duration of the post-hatch development phase appeared to increase with lower humidities experienced by the last three releases of larval lone star ticks (Figure 6). Further work would be necessary to confirm this hypothesis.

Larvae showed no affinity during 1972 for any particular type of plant when ascending the vegetation. They were noted to climb buckbrush (_Symphoricarpus orbiculatus_ Moench), sericea-lespedeza [_Lespedeza cuneata_ (Dumont G. Don)], Virginia wildrye (_Elymus virginicus_ L.), Canada wildrye (_E. canadensis_ L.), johnson grass [_Sorghum halepense_ (L) pers.], purpletop [_Tridens flavus_ (L.) Hitchc.], and broadleaf uniola (_Uniola latifolia_ Michx.). Two larval masses were observed on a dead twig and stick within the arena. Once the ticks had climbed the vegetation within the arena they tended to rest beneath the leaves or on the shaded side of the stem of the plant they had chosen. Larvae could be found within the arenas at heights ranging from 5-76 cm. Most were observed at a height of 30 cm. which placed them within reach of many of their known hosts (Clymer, et al., 1970b).

Once on the vegetation the larval ticks in this study exhibited little movement. Extensive vertical migrations such as those observed by Milne (1946), while working with *I. ricinus*, were not noted in this work with *A. americanum* larvae. Basically, only two types of movement were recorded for larval lone star ticks: (1) avoidance of direct solar radiation; and (2) minor vertical movements stimulated by the presence of a prospective host. One other type of movement was observed in the 1973 study and will be discussed later.

Wilkinson (1953) noted that *B. microplus* larvae tended to show little movement while on the vegetation. Moreover, it appeared that the tendency to remain aggregated was stronger than the stimulus of light, which on shaded supports would come from below. When observed without disturbance larval lone star ticks in the 1972 study could be found resting in tightly clustered masses. This aggregation behavior has been elucidated by Goldsmid (1967) while working with the blue tick, *Boophilus decoloratus* (Koch). Goldsmid speculated on the possibility of secretions playing some part in larval cluster formation. He showed that larvae recognize and choose aggregations of their own species.

If, during the course of observation, the larvae perceived the researcher the cluster quickly took on a "fuzzy" appearance as individuals' legs were thrust in a questing position. Occasionally, as more individuals were stimulated a droplet shaped mass of larvae would form and "drip" to the ground. It is possible that under pristine circumstances this phenomenon could contribute significantly in lowering attachment success by increasing mortality. From the standpoint of this study it was important that the researcher took pains to avoid disturbing the larval masses while making observations.

Factors which shorten the longevity of lone star tick larvae in the field are temperature and humidity. Also included in this category are rainstorms and strong winds. Although the larvae released during July and August of 1972 exhibited significantly shorter life spans (Figure 6), due primarily to increased temperatures and decreased humidities, it is believed that a combination of the aforementioned factors caused the larvae to succumb. This is reflected in Figure 6 which illustrates that other than the July and August extremes, there were no definite survival pattern attributable to any specific factor. At one point, in mid-July, observations were made on successive days between which a rainstorm had occurred. One large mass of seed ticks was apparently removed from the vegetation by the force of the rain, as it was not observed the second day. Subsequent observations revealed no regrouping of the larval cluster. Hair and Howell (1970) have also noted that heavy rains and strong winds tend to dislodge seed tick masses, and they state that under such circumstances less than 19% of the mass has the ability to regroup. Presumably, once the mass of larval lone star ticks which had been observed during 1972 was separated the individuals lost their collective ability to withstand environmental stresses and expired.

Diurnal Behavior of Larval Ticks During August, 1973

During the summer of 1973 a study of larval diurnal behavior was carried out and the results are presented in Table II. From table I one can see that larval *A. americanum* seldom changed position on the vegetation during the daylight hours. Only twice during the course of the experiment were any ticks in direct sunlight and both of these were noticed while making the morning observations. Although neither group

TABLE II

RESULTS OF OBSERVATIONS MADE THREE TIMES DAILY ON UNFED LONE STAR TICK LARVAE IN FOUR HABITAT TYPES FOR A FIVE DAY PERIOD DURING AUGUST, 1973

6 Aug

	1[a/]	2	3	4
0900[b/]	A[c/]	A		
1400	A	A		
2100	B	B		

7 Aug

	1	2	3	4
0900	A	A[d/]	A	
1400	B	A	A	
2100	C	B	B	

8 Aug

	1	2	3	4
0900	A	A	A	A
1400	A	B	A	A
2100	A	C	C	A

7 Aug

	1	2	3	4
0900	A	A	A	A
1400	A	A	A	A
2100	B	B	B	B

10 Aug

	1	2	3	4
0900	A	A	A	A
1400	A	A	A	A
2100	A	A	B	B

a/ Habitat types: 1 - upland oak-hickory
2 - meadow
3 - bottom oak-hickory

b/ Time of observation.

c/ Observations represented by a letter different from the letter representing the preceding observation indicates tick movement.

d/ In sunlight at time of observation.

had moved when the subsequent observation was made, both were in the shade due to the movement of the sun.

A conspicuous feature of the observations was the movement at dusk of the larval groups into more exposed positions. The larvae would often move around to the upper leaf surface or to the terminal portion of the leaf. Wilkinson (1953) noted similar behavior by larval *B. microplus* on *Paspalum dilatatum* but offered no explanation as to the reason for this behavior. There may have been various factors causing this behavior, including: (1) to take advantage of cool nocturnal temperatures and high humidities; and (2) obtain maximum exposure at a time when most of their preferred hosts will be active. A third possibility may have been that with the stimulus of light removed the ticks no longer remained on the shaded portions of the plant. Table II shows that the larval clusters had, in all cases, moved into concealment by the time of the morning observation.

Effect of Climatic Factors on Fed Female Ticks During 1972

Immediately after release into the upland oak-hickory habitat the replete female ticks began moving through the leaf litter into the duff layer (the layer of decaying leaf litter and detritus immediately above the soil). On observations subsequent to their release the ticks were noted to be active and moving from one potential oviposition site to another. Limiting observations to one per week lessened disturbance and allowed the females to become quiescent and remain at one site.

Sweatman (1967) defines the pre-oviposition period of an engorged tick as the number of days from engorgement to the first day of egg laying. Figure 7 shows that the pre-oviposition period of the ticks in 1972 decreased steadily with each group of ticks released from April to late July. The reason for this decreasing of the pre-oviposition period was probably increasing temperatures, as noted by Sweatman (1967) and Hooker, et al., (1912). It would appear that the effect of low humidities in increasing the pre-oviposition period (Lancaster and MacMillan, 1955; Lancaster, 1957; Arthur, 1951) was overshadowed by the rising summer temperatures. It has been shown that high temperatures and low humidities are characteristic of late Oklahoma summers (Figures 11 and 12, Appendix). Although no work concerning the effect of photoperiod on the lone star ticks has been done, Wright (1971) showed that there was no influence on the pre-ovipositional behavior of _A. maculatum_, a closely related species.

Of the ticks which were known to have oviposited, 94% placed their egg masses in the leaf litter or the duff layer. The remaining 6% were found to have placed their eggs in indentations in the soil which they had apparently scratched out. Similar observations were recorded by Lancaster (1973).

Egg incubation data indicates that, with the exception of the April release, all larval ticks hatched and were observed ascending vegetation within 2-3 weeks of each other from 26 August to 15 September 1972. Hair (unpublished data)[3] states that lone star tick eggs kept at 20°C and 30% RH hatched, but there was no larval survival. Hair also found that those eggs kept at 60% RH hatched and the resulting larvae survived for a short period of time. Lancaster and MacMillan (1955) and

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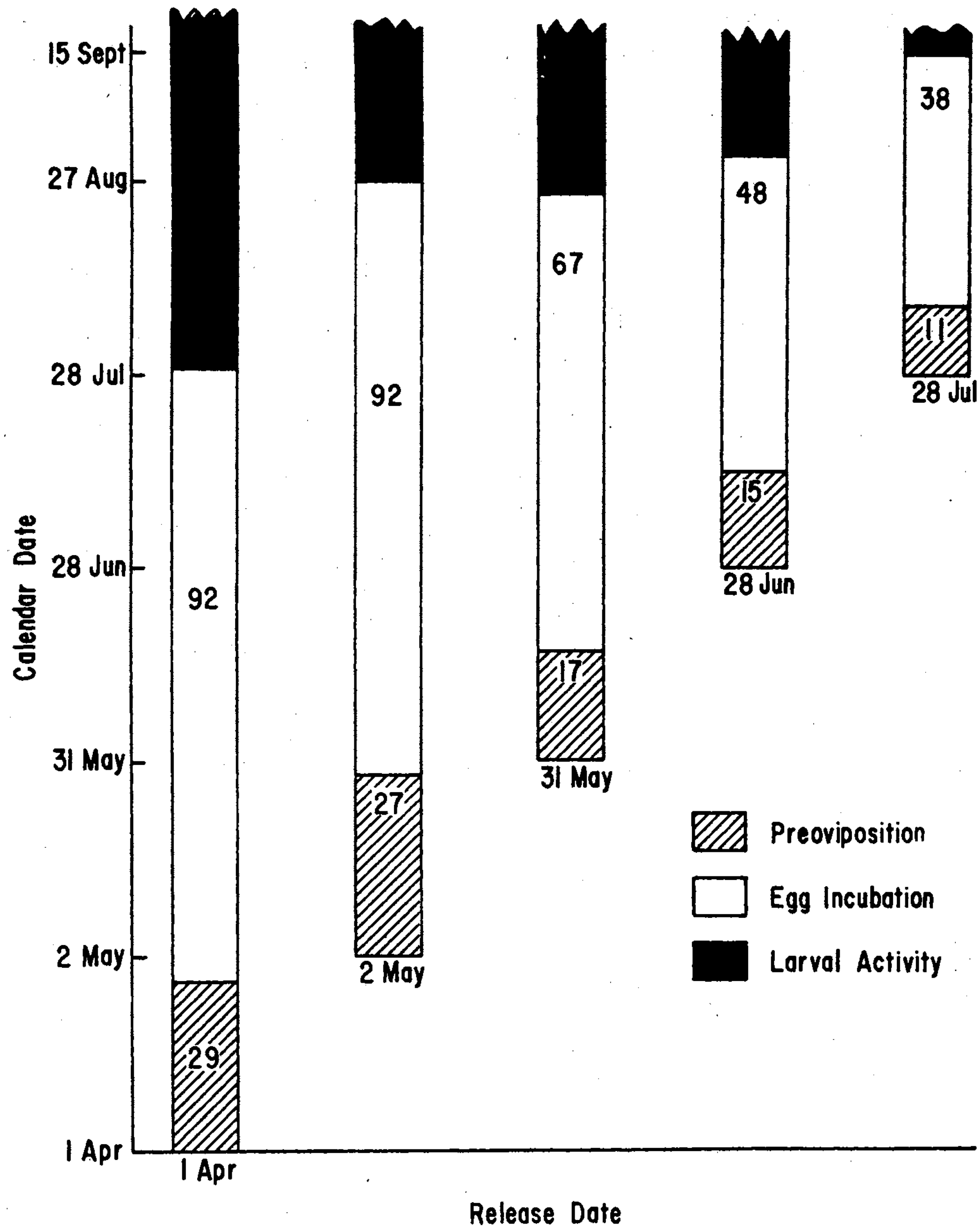
[3]Unpublished data. J. A. Hair. Associate Professor, Department of Entomology, Oklahoma State University, Stillwater, 74074

Figure 7. Results of Observations on Replete Female Lone Star Ticks in an Upland Oak-Hickory Habitat Type in the Cookson Hills Game Refuge, Oklahoma, During 1972



15 Sept
27 Aug
28 Jul
28 Jun
31 May
2 May
1 Apr
Calendar Date
29
92
27
92
17
67
15
48
11
38
1 Apr
2 May
31 May
28 Jun
28 Jul
Release Date
Preoviposition
Egg Incubation
Larval Activity

Lancaster (1957) found that hatching time of lone star tick eggs varied directly with humidity at values above 65% RH. This may represent a mechanism within the egg itself which allowed the eggs laid early in the season during 1972 to hatch at a more favorable time. Since it is known that larval ticks are highly susceptible to dessication at high temperatures and low humidities (Feldman-Muhsam, 1947) it would be to their advantage to hatch during a period of decreasing temperatures and rising humidities. This same response may have served to synchronize the onset of larval activity. Larvae from each of the releases were noted to be active when observed last in mid-September (Figure 7). Figure 8 illustrates the fate of each of the replete female lone star ticks released during 1972 and the data is summarized in Table III. An average of 20% of the released females were not found on observations subsequent to their release. It is doubtful that the unobserved ticks escaped the arenas, rather it is more likely they were removed by some other organism or were simply overlooked. Care was taken during observations to minimize disturbance and, thus, the thorough search necessary to locate the missing ticks was not allowed.

An average of 18% of those ticks found did not oviposit. Included in this number were 7% of the ticks which were apparently devoured, punctured, or otherwise killed by unknown organisms before they had the opportunity to do so. Lancaster and MacMillan (1955) showed that replete female lone star ticks either fail to oviposit or the eggs are not viable at humidities below about 65%. One would assume that if low humidities were causing oviposition failure it would have been apparent in a larger percent of the sample. This, in addition to the fact that no unhatched egg masses were found upon termination of the study, would

Figure 8. Fate of all Replete Female Lone Star Ticks Released into an Upland Oak-Hickory Habitat Type in Eastern Oklahoma During 1972

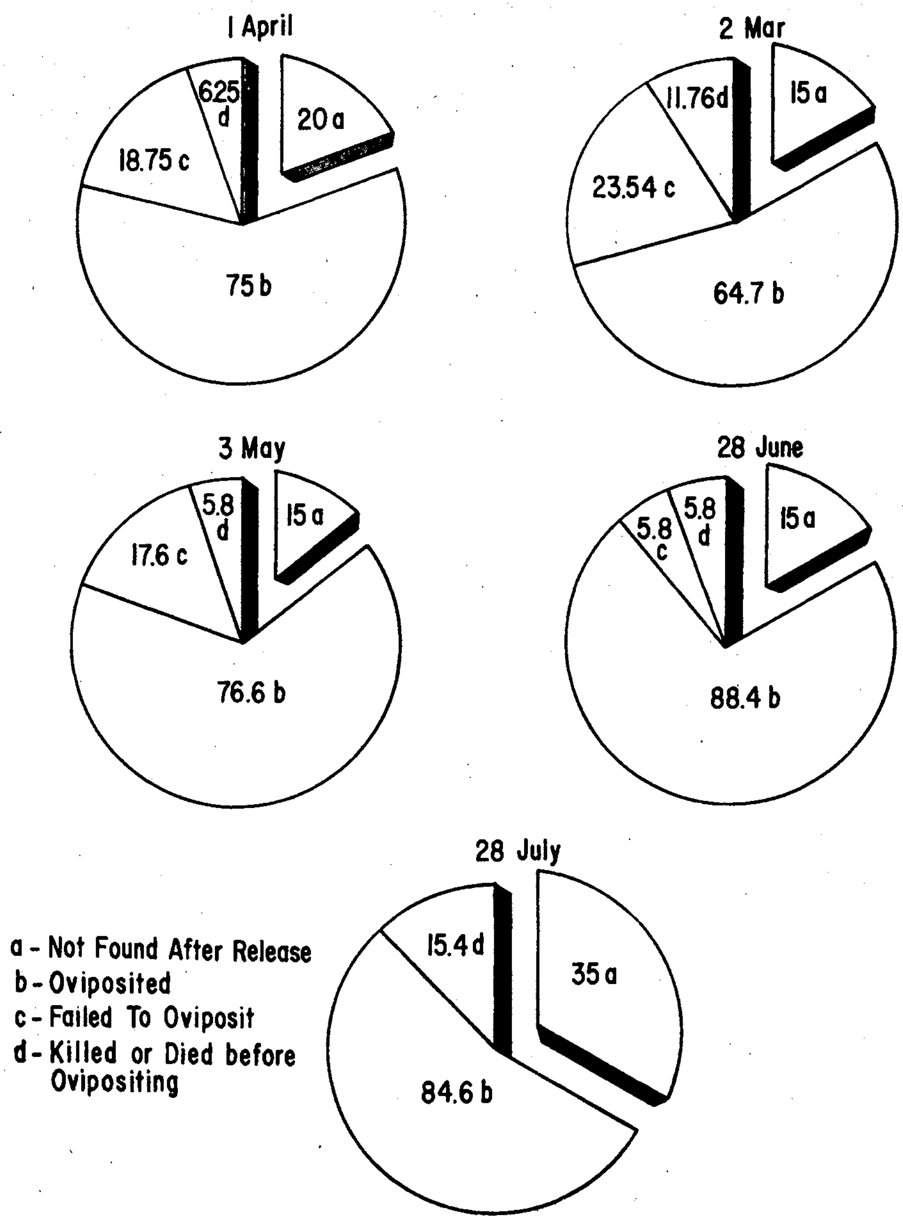

1 April
6.25 d
20 a
18.75 c
75 b
2 Mar
11.76d
15 a
23.54 c
64.7 b
3 May
5.8 d
15 a
17.6 c
76.6 b
28 June
5.8 c
5.8 d
15 a
88.4 b
28 July
15.4 d
35 a
84.6 b
a - Not Found After Release
b - Oviposited
c - Failed To Oviposit
d - Killed or Died before Ovipositing

TABLE III

SUMMARY OF DATA ON REPLETE FEMALE LONE STAR TICKS PLACED INTO UPLAND OAK-HICKORY HABITAT TYPES, COOKSON HILLS GAME REFUGE, CHEROKEE COUNTY, OKLAHOMA, 1972

	Release Date					
	1 April	2 May	31 May	28 June	28 July	Mean ($\bar{x}$)
Not found	20[a]	15	15	15	35	20
Oviposited	75	64.7	76.5	88	84.6	77.8
Failed to Oviposit	18.75	23.5	17.6	5.8	0	13.1
Found Dead Before Ovipositing	6.25	11.76	5.8	5.8	15.4	9.0

a/ All values are expressed as % of the total release.

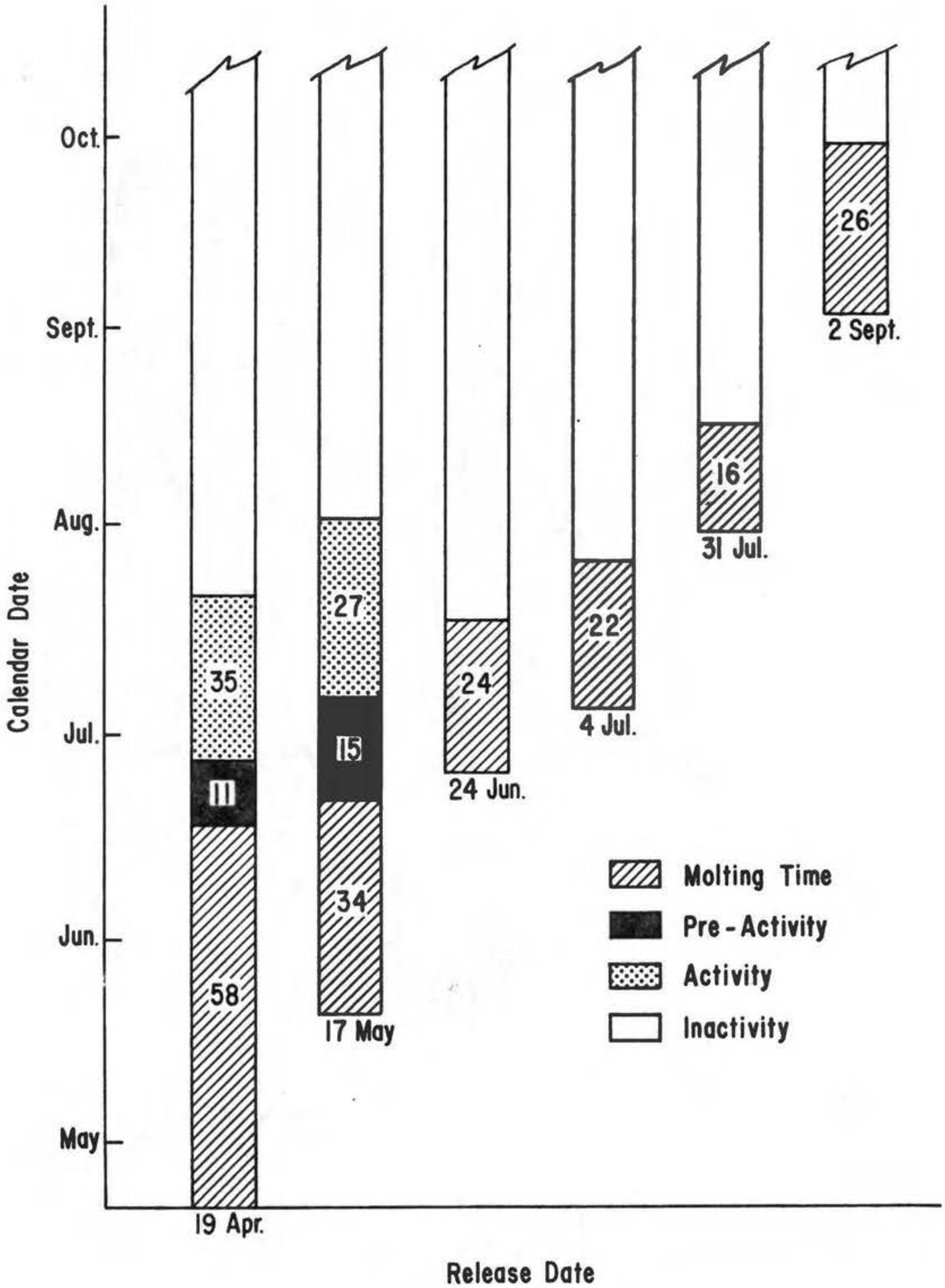
lead one to believe that some factor other than humidity had caused this ovipositional failure.

Effect of Climatic Factors on Fed
Nymphal Ticks During
1972 and 1973

It was noted in these studies, and by other researchers (Balashov, 1973), that after dropping off the host, mobility of completely engorged ticks was limited due to enlargement of the body. Negative phototactic and positive thigmotactic responses caused the ticks to hide in plant litter and other shelters immediately upon detachment from the host and falling to the ground (Balashov, 1972). In my study, engorged nymphal lone star ticks quickly became quiescent and remained in that state until ecdysis. Hooker, et al. (1912) felt that a total effective temperature of 657°F was required to transform replete nymphs to adults. Using Hooker's calculated mean effective temperature, replete nymphs exposed to 80°F should molt after 18 days. According to Hair and Howell (1970) this method of calculating molting time is, in reality, accurate.

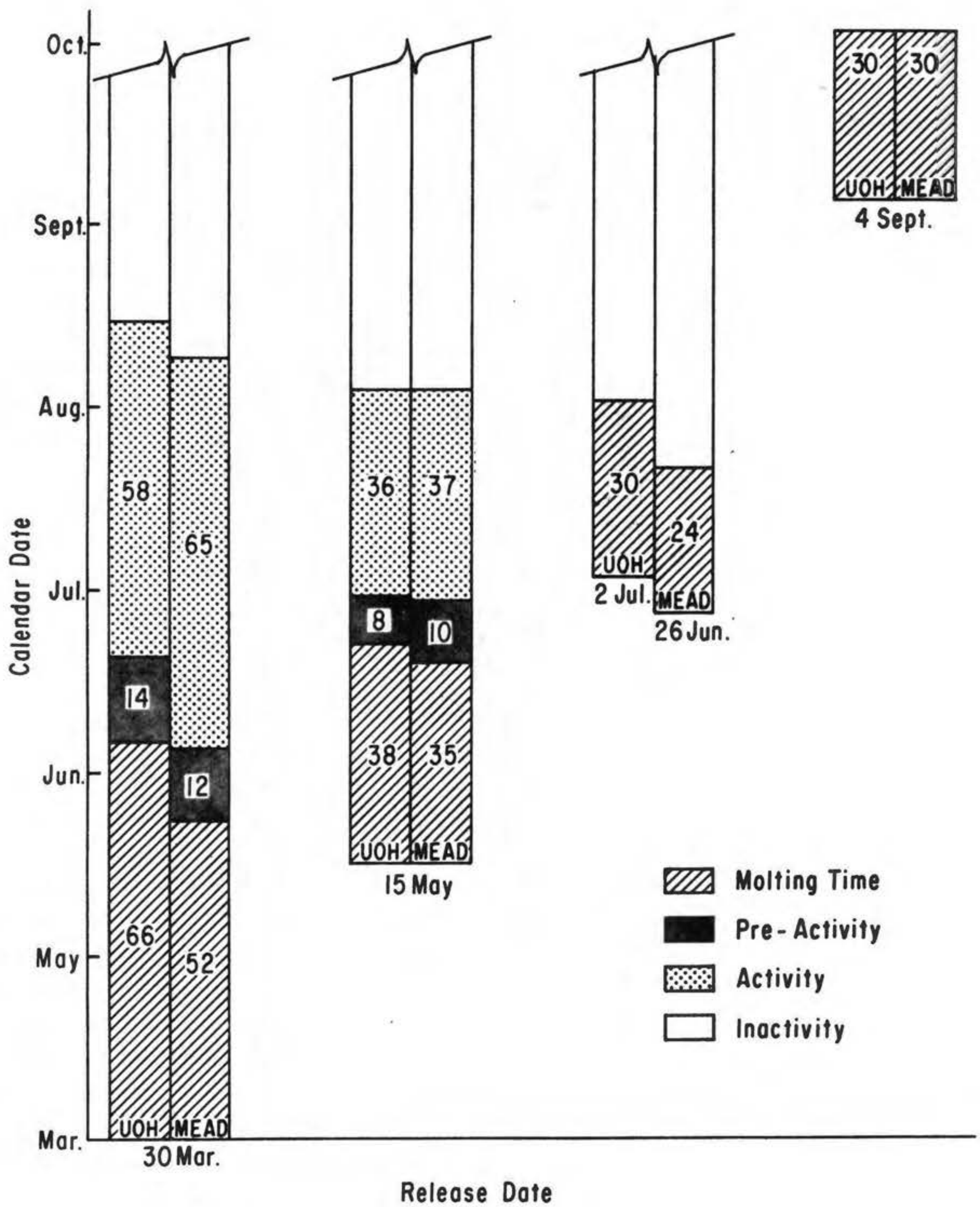
In comparing Figures 9 and 10 it can be seen that the time required for molting was generally shorter during the 1972 study period. During 1972 the least amount of time required for molting was 16 days by the ticks released 31 July 1972, whereas the least amount of time required during 1973 was 24 days by the 26 June release in the meadow. Similar variation has been noted by Hooker, et al. (1912) who reported as much as 2-3 weeks difference in average molting time from year to year. Semtner, et al. (1973c) published a study similar to the present one in which replete nymphal lone star ticks released in late June required 29

Figure 9. Behavior of Engorged Nymphal Lone Star Ticks Released into an Upland Oak-Hickory Habitat Type in Cherokee County, Oklahoma, During 1972



Oct.
Sept.
Aug.
Jul.
Jun.
May
Calendar Date
26
2 Sept.
16
31 Jul.
22
4 Jul.
24
24 Jun.
27
15
34
17 May
35
11
58
19 Apr.
Molting Time
Pre - Activity
Activity
Inactivity
Release Date

Figure 10. Behavior of Engorged Nymphal Lone Star Ticks Released into Two Habitat Types, Meadow and Upland Oak-Hickory, in Cherokee County, Oklahoma, During 1973



Oct.
Sept.
Aug.
Jul.
Jun.
May
Mar.
Calendar Date
58
65
14
12
66
52
UOH
MEAD
30 Mar.
36
37
8
10
38
35
UOH
MEAD
15 May
30
24
UOH
2 Jul.
MEAD
26 Jun.
30
30
UOH
MEAD
4 Sept.
Molting Time
Pre-Activity
Activity
Inactivity
Release Date

days to complete ecdysis.

Figure 10 shows that, with the exception of the 4 September release, the ticks in the meadow habitat required shorter periods of time than those in the upland oak-hickory before molting occurred (an average of 35 days in the meadow as compared to 41 days in the oak-hickory). Because it has been shown (Figure 14, Appendix) that meadow temperatures were generally somewhat higher than those in the oak-hickory habitat it is presumed that this allowed more rapid post-engorgement development.

No ticks in these studies entered the winter unmolted. It has been noted that engorged nymphs dropping in early October probably will not molt (Semtner, et al., 1973c). Further observations the following season indicated that those ticks overwintering as engorged nymphs experienced 90% mortality and no unmolted ticks were found.

It was noted (Figures 9 and 10) that engorged nymphal lone star ticks molting after mid- to late July did not become active during the same season. This is consistent with data presented by Semtner, et al. (1973c). In addition, Semtner noted that the ticks which did become active represented a small percentage of the total number released. It was observed in the 1973 study that a relatively small number of the newly molted ticks responded to disturbance by the researcher (20%, meadow; 7.3%, upland oak-hickory). The maximum percentages of active ticks were observed in mid-July and were ticks from the 30 March, 1973 release. Sonenshine and Levy (1971) theorized that newly molted adults fail to become active during the first season following the molt. Semtner, et al. (1973c) concluded, and the data on Figures 9 and 10 support his contention, that Sonenshine and Levy were correct in that the majority of those ticks which molt after mid-July remain inactive during their first summer. A small percentage of those ticks molting before mid-July exhibited host seeking behavior. Newly molted adult ticks became active following a period of inactivity. During this period (post-molt development phase) the ticks were noted upon disturbance to move back to the underside of fallen leaves, indicating negative phototactic and positive geotactic responses. Balashov (1972) states that this behavior is characteristic of ixodid ticks. During this stage experimental stimulation of corresponding chemo-, thermo-, and mechano-receptors in *I. ricinus* did not produce the typical waiting postures or questing behavior (Lees, 1948).

In 1972 (Figure 9) the duration of the post-molting development phase increased from 11 to 15 days with the second release. Conversely, the time spent in this stage by the 1973 ticks in both habitat types (Figure 10) decreased with the second release (from 14 days to 8 days in the forest and from 12 days to 10 days in the meadow). These minor differences in post-molt development periods could have been a result of latitude in observation dates.

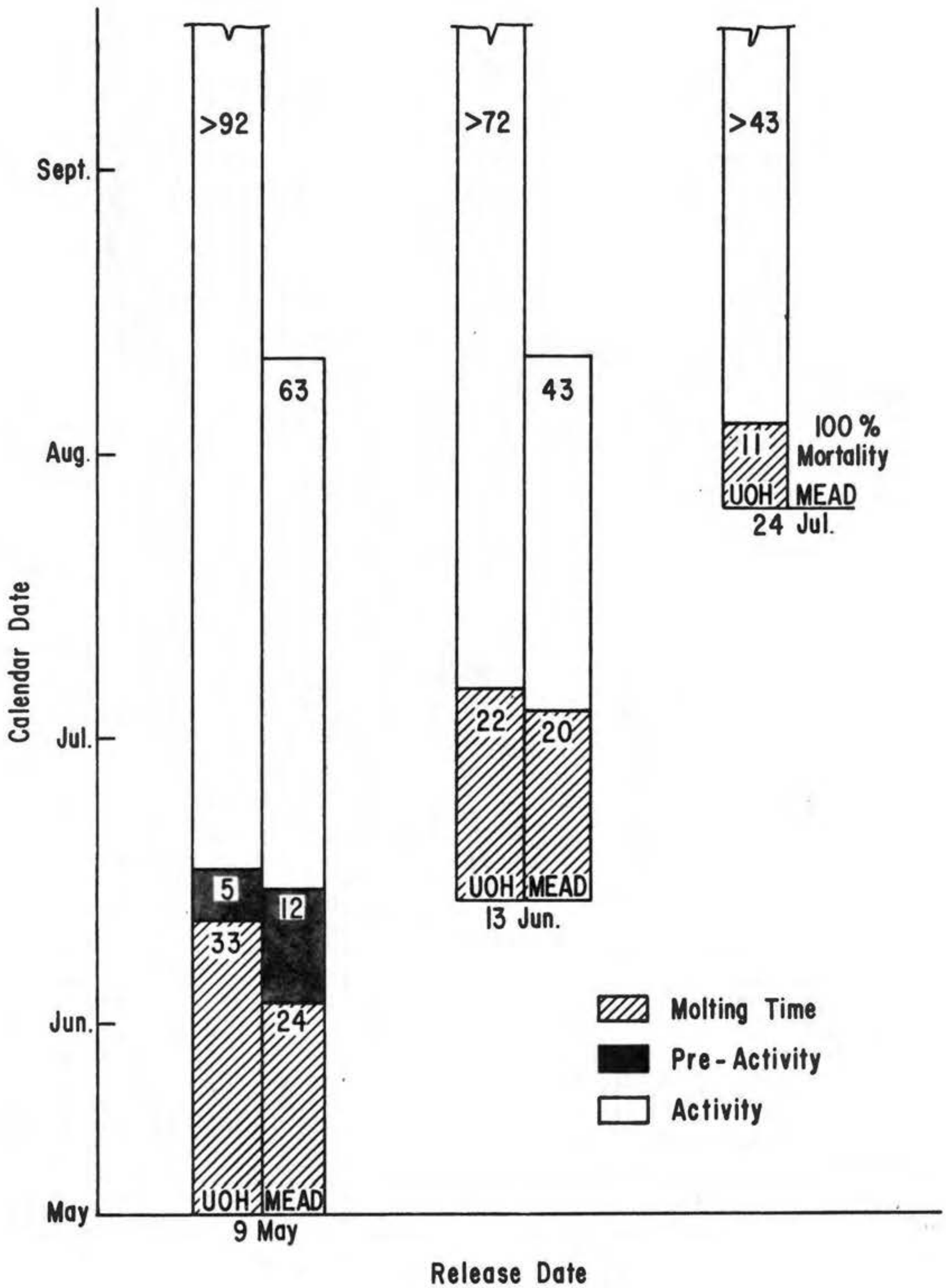
Effect of Climatic Factors on Fed Larval Lone Star Ticks

Engorged larvae exhibited similar behavior patterns as those shown by engorged nymphs. Immediately after release they were noted to move into the leaf litter. The larvae then remained immobile until ecdysis. This was not unlike engorged nymphal behavior and similar behavior was reported for both these stages by Balashov (1972).

According to Balashov, molting time of engorged larvae is controlled primarily by temperature, as is nymphal molting time. Hooker, et al. (1912) had found the total effective temperature required to induce molting from the larval to the nymphal stage to be 350°F. This is considerably less than that required to transform nymphs to adults (657°F). In comparing the data on engorged larvae (Figures 11 and 12) with that on engorged nymphs (Figures 9 and 10) one will notice that engorged larvae released on similar dates required somewhat less time before molting.

A general trend toward decreasing molting times was shown in the 1972 releases, with those ticks in the meadow requiring less time to molt than those released in the oak-hickory habitat on the same date (Figure 11). A mortality rate of 100% was observed in the ticks released in the meadow habitat on 24 July 1972. This mortality was probably due to the high temperatures experienced during that part of the season. Engorged larvae released exactly one year later during 1973 were noted to have experienced some mortality (21%) but the remainder were able to successfully molt to the nymphal stage. Lancaster and MacMillan (1955) have shown that engorged larval lone star ticks failed to molt and succumbed at relative humidities below 69%. Since the relative humidities experienced during the 1973 study period were probably higher than during the 1972 study period due to increased rainfall (Table IV and V, Appendix), the ticks in the 24 July 1973 release experienced lower mortality and were able to molt to the nymphal stage. The ticks released into the oak-hickory habitat on the same date (24 July) required only 11 days to molt into nymphs. This was the shortest time recorded during the 1972 and 1973 study periods although Hooker, et al. (1912) reported that engorged larval lone star ticks may

Figure 11. Behavior of Engorged Larval Lone Star Ticks Released into Two Habitat Types, Meadow and Upland Oak-Hickory, in Cherokee County, Oklahoma, During 1972



Sept.
Aug.
Jul.
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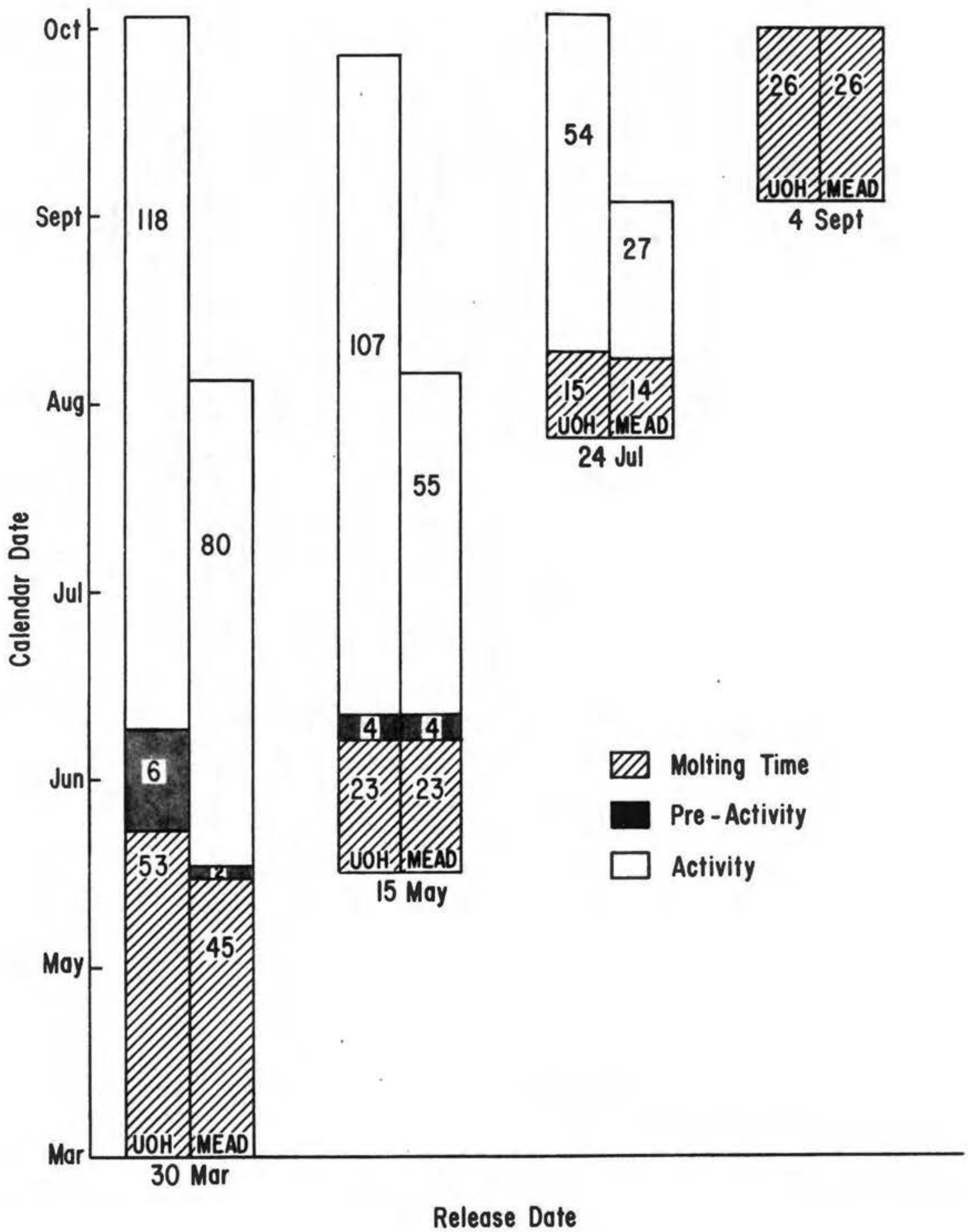
May
Calendar Date
>92
63
5
12
33
24
UOH
MEAD
9 May
>72
43
22
20
UOH
MEAD
13 Jun.
>43
11
100 %
Mortality
UOH
MEAD
24 Jul.
Molting Time
Pre-Activity
Activity
Release Date

Figure 12. Behavior of Engorged Larval Lone Star Ticks Released into Two Habitat Types, Meadow and Upland Oak-Hickory, in Cherokee County, Oklahoma, During 1973



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Calendar Date
118
6
53
UOH
80
2
45
MEAD
30 Mar
107
4
23
UOH
55
4
23
MEAD
15 May
54
15
UOH
27
14
MEAD
24 Jul
26
UOH
26
MEAD
4 Sept
Molting Time
Pre-Activity
Activity
Release Date

molt as soon as 7 days after detachment from the host. The first and last of the 1973 releases were indicative that ecdysis was hampered by the cool temperatures experienced by ticks engorging in early spring or late summer.

According to Balashov (1972) the pre-activity period (post-molt development phase) required by newly molted adults is always longer than that required by the immature stages. This is consistant with data presented herein. The post-molt development phase appears to have been governed by temperature as was the length of time required for molting. As can be seen in Figures 11 and 12 the length of the pre-activity period was shortened with each successive release. During 1972 the pre-activity period required by the first release of fed larval ticks was 5 and 12 days in the oak-hickory and meadow habitats, respectively. No pre-activity period was observed with releases subsequent to the 9 May release. Similar results were noted with the ticks released during the 1973 study period. This corresponds with the increasing temperatures experienced as the season advanced (Figures 13 and 14, Appendix). In the latter releases in which activity ensured the post-molt development phase was so short as to be unobservable or nonexistent. This may indicate that under field conditions newly-molted nymphs are able to seek and attach to a host almost immediately after emerging. Hair and Howell (1970) reported that some newly hatched larval lone star ticks feed almost immediately and it may be that under conditions of high temperature and low humidity that newly-molted nymphal ticks exhibit a similar response.

Without exception, ticks in the upland oak-hickory habitat type remained active after-mid-September in both 1972 and 1973. Regardless of molting date, the ticks in the oak-hickory habitat during 1973 remained active until October (Figure 12). Cooling temperatures were probably the cause of the cessation of activity at that time.

In contrast to the ticks in the oak-hickory habitat newly-molted nymphs in the meadow showed a somewhat curtailed active period. This held true for ticks released both in 1972 and 1973. Figures 11 and 12 indicate that those ticks molting in the meadow before mid-July were active until mid-August or an average of 62 days. The ticks released 24 July 1973 were molted by the first of August and then became active for a period of 27 days. It would appear then, in comparing the meadow with the oak-hickory habitat types, that high temperatures in combination with the lower daytime humidities which characterize the meadow, made it a less favorable habitat and thereby limited the activity of lone star ticks occurring there.

Hair and Howell (1970) stated that the unfed larval population peaked around 1 August with high numbers being found through September. These same workers noted that nymphal lone star ticks may overwinter either as unfed nymphs or fed larvae. Larvae engorging as late as 4 September molted and entered the winter as unfed nymphs (Figure 12), but the time required for molting was lengthened by the cooler temperatuers and nymphs were not active their first season.

CHAPTER V

SUMMARY AND CONCLUSIONS

This work was begun during 1972 to help elucidate the field behavior of the lone star tick, *Amblyomma americanum* (Linneaus) in eastern Oklahoma. The seasonal activity and behavior of unfed lone star ticks of all stages in different habitat types was recorded. Observations were also made on the diel behavior of unfed larval lone star ticks. Environmental parameters recorded included temperature at various levels, relative humidity, and photoperiod.

Behavior of the fed stages of the lone star tick in different habitat types was studied during 1972 and 1973. Molting time, time required for the post-molt development phase, and length of activity of newly molted nymphs and adults was recorded for engorged larval and nymphal lone star ticks in different habitat types. Engorged female lone star ticks were released in the field and initial oviposition time, hatching time, and onset of larval activity was observed. Fed ticks were released at various intervals from March to September.

Numbers of adult ticks observed to be active declined with rising temperatures and falling humidities. The ascent and subsequent descent of the vegetation by adult lone star ticks in the oak-hickory habitat could not be correlated with photoperiod. Mortality of ticks in the meadow habitat probably was high due to high temperatures and low humidities. Observations on individual ticks showed them to have periodic phases of inactivity.

Activity of unfed nymphs may have been significantly influenced by relative humidity in 1973. High temperatures in the meadow habitat probably forced the ticks to remain at the vegetation tips from early June until activity had ceased.

Unfed larval lone star ticks were shown to be susceptible to adverse environmental conditions of high temperatures and low relative humidities. After ascension of the vegetation little larval movement was noted. It was noted that larvae tended to move into a position of maximum exposure after dusk and returned to their original position before 0900 the following day.

The time required by engorged females for pre-oviposition and egg incubation was shown to be shortened by increasing temperatures.

Molting time of engorged larvae and nymphs was probably dependent primarily on temperature. Ticks in the meadow habitat required less time to complete molting. Engorged larvae required less time for post-molt development than engorged nymphs. Only nymphs molting to adults before mid-July became active, whereas, nymphs molting from engorged larvae as late as 6 August became active. Activity of newly molted ticks in the meadow was generally shorter than that in the upland oak-hickory habitat type.

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TABLE IV

MEAN DAILY PRECIPITATION IN EASTERN OKLAHOMA[a/]
FROM APRIL THROUGH SEPTEMBER, 1972

Date		Precipitation/Monthly Total (mm)
April	13	4.06
	14	7.11
	15	11.4
	20	18.5
	21	59.69
	27	18.79/119.55
May	1	17.52
	2	10.16
	13	7.11
	17	13.97
	24	4.57
	29	10.41/63.74
June	13	8.89
	14	3.05
	15	29.21
	20	8.89
	23	9.5
	24	9.9
	25	7.8
	26	3.4
	27	22.6
	28	37.08/139.96
July	2	9.39
	3	19.05
	4	4.3
	13	18.79
	14	24.63/76.16
August	5	9.14
	22	3.81
	23	11.43
	25	9.39
	31	8.64/42.41
September	1	8.38
	5	3.3
	21	9.39
	22	15.24
	23	28.95
	27	16.76
	30	5.5/87.52
Total Precipitation		529.34 mm

[a/] Means of climatological data for Sallisaw, Tenkiller Dam, Stilwell, and Tahlequah weather stations. U. S. Dept. of Commerce, 1972, Climatological Data, Oklahoma. Vol. 81. Superintendent of Documents, Government Printing Office, Washington, D. C.

TABLE V

MEAN DAILY PRECIPITATION IN EASTERN OKLAHOMA[a/] FROM APRIL THROUGH SEPTEMBER, 1973

Date		Precipitation/Mo. Total (mm)	Date		Precipitation/Mo. Total (mm)
April	3	14.5	July	5	16.51
	4	5.0		11	6.35
	7	4.3		15	3.81
	8	2.5		17	11.17
	9	12.44		18	2.54
	15	3.3		25	10.66
	16	57.66		29	9.39
	20	12.44		30	3.04
	22	58.42		31	5.58/69.05
	23	11.4	August	11	42.41
	26	4.8		12	7.62
	27	6.6/193.36		16	33.02
May	2	15.2		30	15.24/98.29
	7	31.75	September	2	8.38
	12	4.57		5	22.6
	22	12.44		6	19.3
	23	11.68		7	5.58
	24	12.19		9	13.72
	27	34.54		13	27.17
	31	32.76/155.13		25	37.08
June	1	9.14		26	42.42
	2	16.0		27	4.32
	3	57.9		28	55.37
	5	20.32		30	3.3/239.24
	14	8.6			
	15	3.3	Total Precipitation		997.81
	17	33.0			
	19	18.79			
	20	20.32			
	27	12.19			
	30	43.18/242.74			

[a/] Means of climatological data for Sallisaw, Tenkiller Dam, Stilwell, and Tahlequah weather stations. U. S. Dept. of Commerce, 1972, Climatological Data, Oklahoma. Vol. 81. Superintendent of Documents, Government Printing Office, Washington, D. C.

TABLE VI

ADULT TICKS FROM SEPARATE RELEASES RESPONDING TO HUMAN BREATH DURING THE 1972 STUDY PERIOD

	Release Date				
Calandar Date	6 April	12 May	10 June	7 July	11 August
April 20	24[a/]				
28	34				
May 4	34				
11	29				
18	30	34			
25	29	27			
June 1	35	36			
8	28	31			
15	28	28	26		
23	28	24	25		
30	27	20	25		
July 6	19	17	17		
13	21	19	20	30	
20	15	19	18	26	
27	10	9	9	15	
August 4	8	6	7	10	
17	3	4	5	5	7
September 3	1	1	1	1	0
15	2	2	1	2	2

a/ Represents the number of ticks observed to be active.

TABLE VII

NYMPHAL LONE STAR TICKS FROM SEPARATE RELEASES RESPONDING TO HUMAN BREATH DURING THE 1972 STUDY PERIOD

	Release Date			
Calendar Date	13 April	17 May	10 June	7 July
April 20	12[a/]			
28	44			
May 4	32			
11	45			
18	26	35		
25	34	27		
June 1	33	34		
8	28	23		
15	25	22	23	
23	22	21	20	
30	20	20	16	
July 6	21	18	18	
13	13	17	19	23
20	6	6	11	13
27	7	5	5	6
August 4	6	3	4	8
17	2	0	9	6
September 3	1	1	4	1
15	1	0	1	1

a/ Represents the number of ticks observed to be active.

Figure 13. Climatic Data Gathered in the Cookson Hills Game Refuge, Oklahoma, During the 1972 Study Period with Mean Daily Temperatures and Relative Humidity Calculated From Hygro-Thermograph Recordings

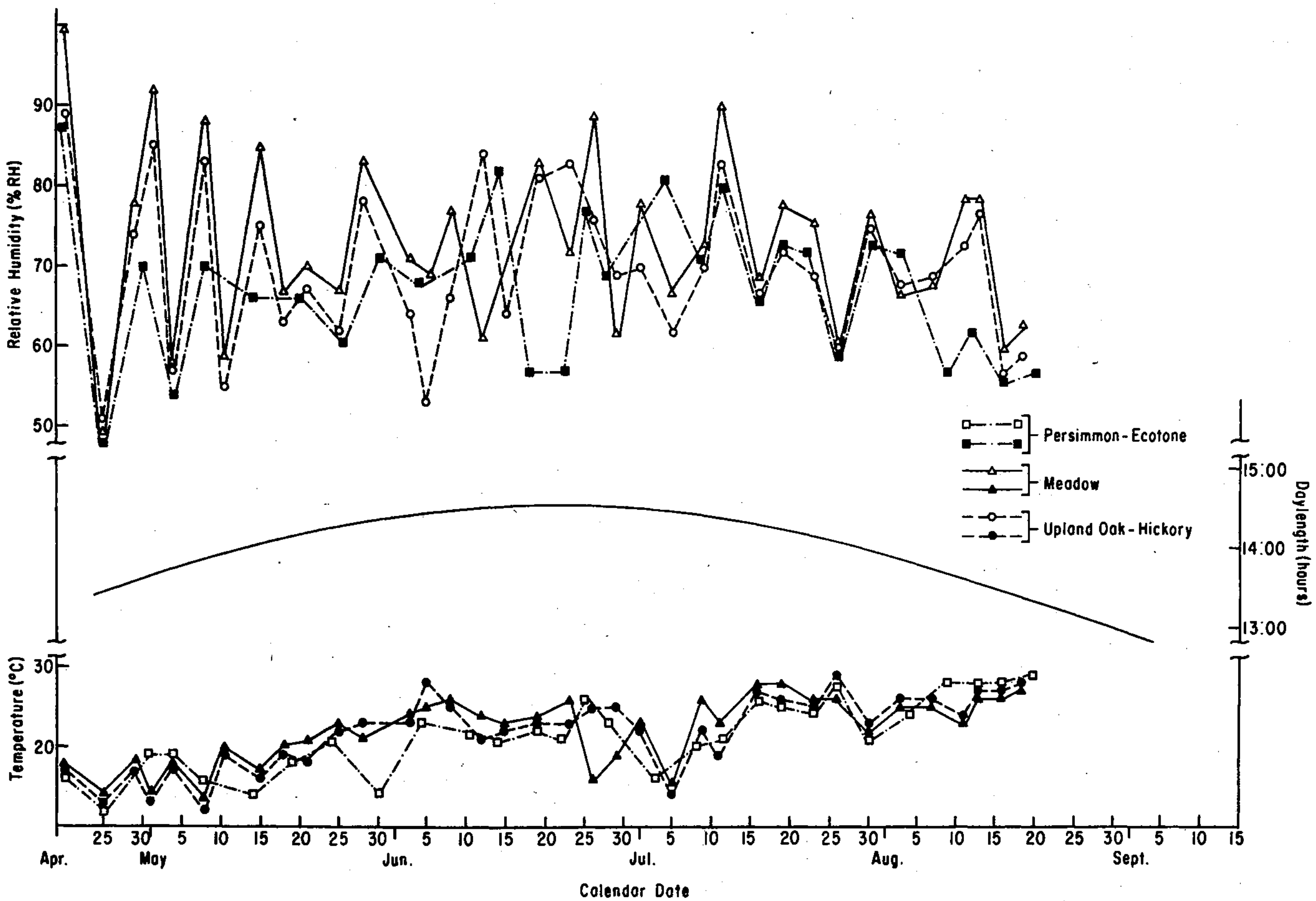

Relative Humidity (% RH)
90
80
70
60
50
Persimmon - Ecotone
Meadow
Upland Oak - Hickory
15:00
14:00
13:00
Daylength (hours)
Temperature (°C)
30
20
25
30
5
10
15
20
25
30
5
10
15
20
25
30
5
10
15
20
25
30
5
10
15
20
25
30
5
10
15
Apr.
May
Jun.
Jul.
Aug.
Sept.
Calendar Date

Figure 14. Climatic Data Gathered in the Cookson Hills Game Refuge, Oklahoma, During the 1973 Study Period with Mean Daily Relative Humidity Calculated From Hygro-Thermograph Recordings and Temperature Measured at Two Levels Using a YSI Telethermometer[R]

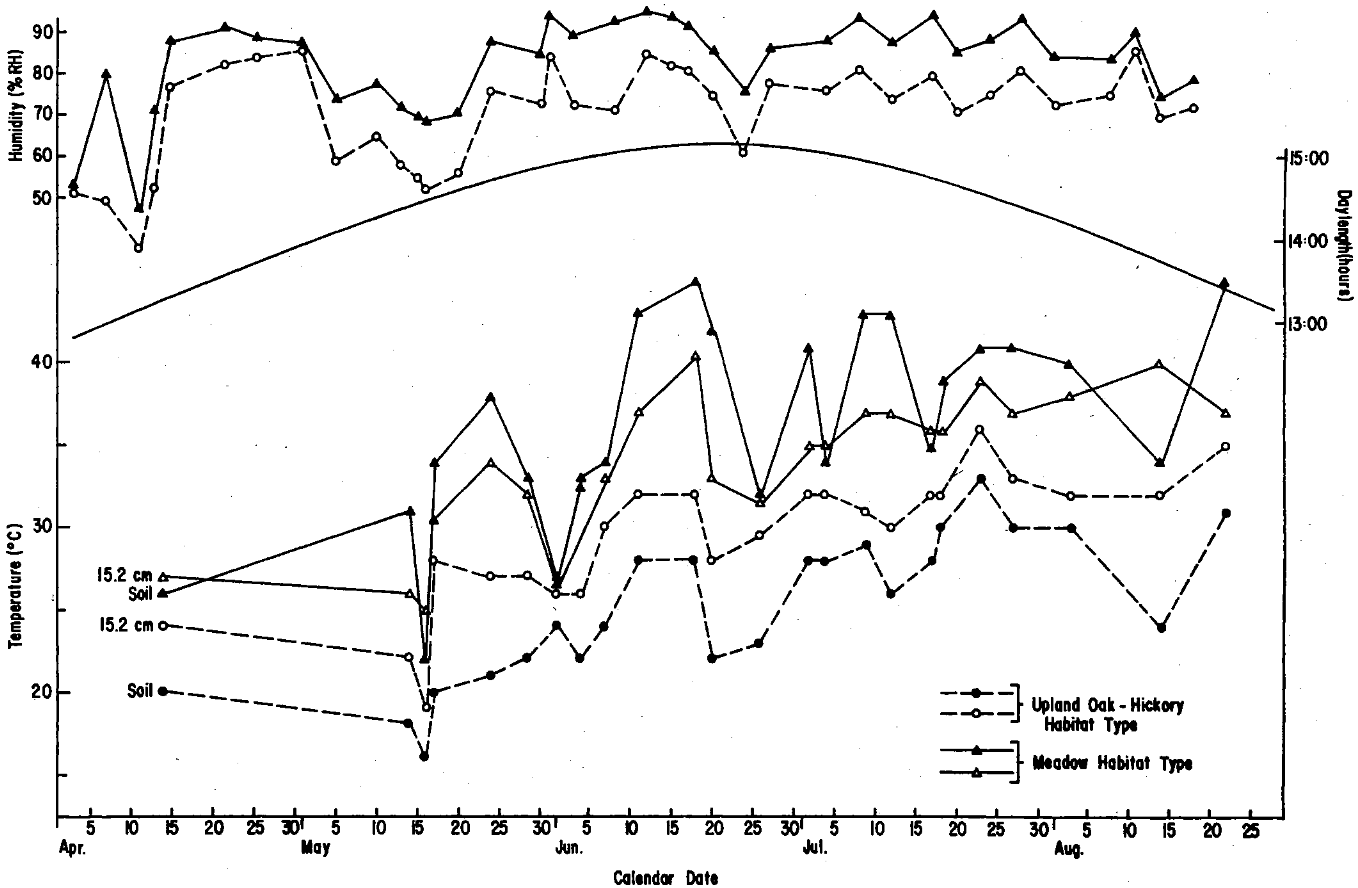
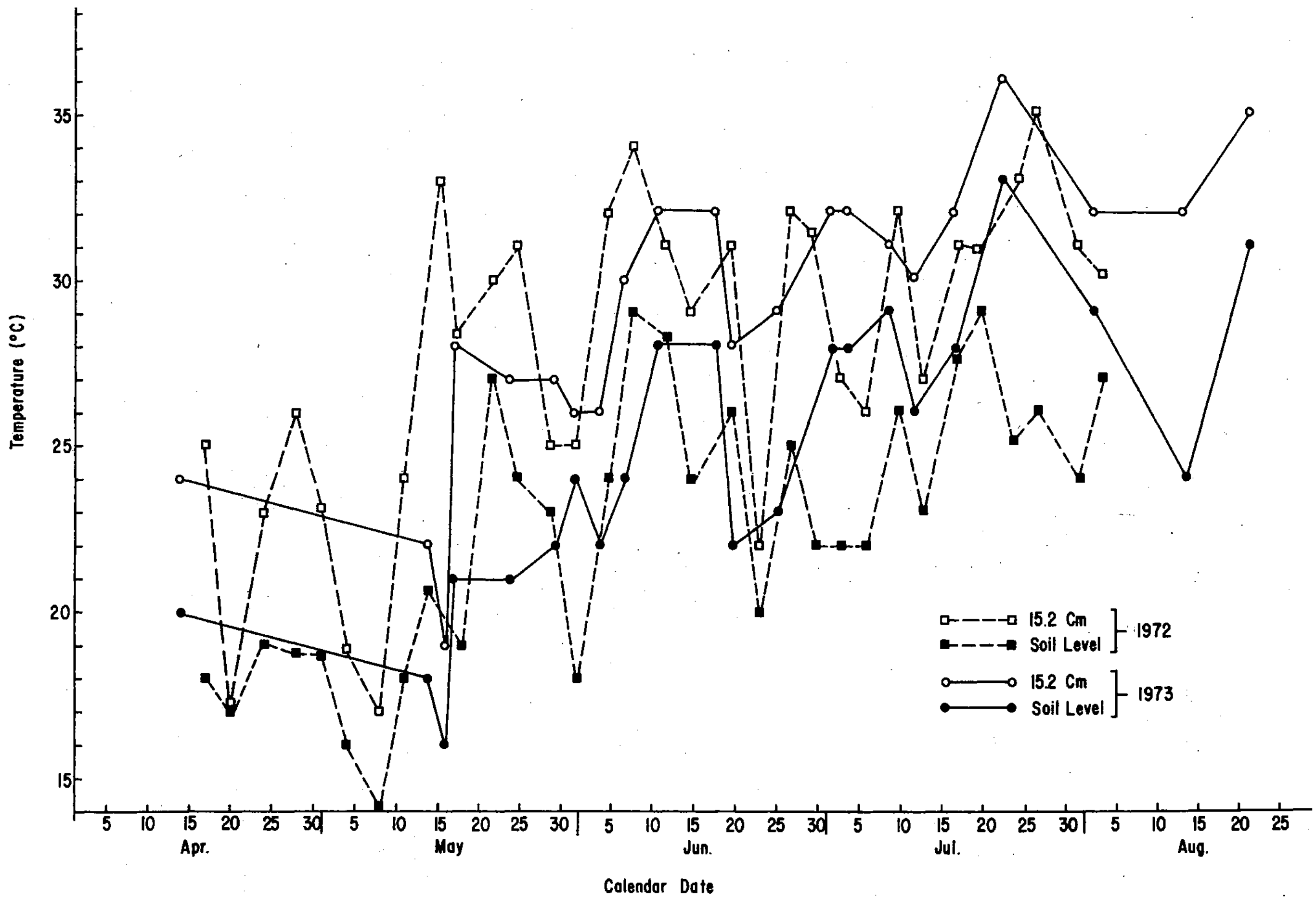

Humidity (% RH)
90
80
70
60
50
Daylength (hours)
15:00
14:00
13:00
Temperature (°C)
40
30
20
15.2 cm
Soil
15.2 cm
Soil
Upland Oak - Hickory Habitat Type
Meadow Habitat Type
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25
Apr.
May
Jun.
Jul.
Aug.
Calendar Date

Figure 15. Temperature Data Gathered During the 1972 and 1973 Study Periods in Upland Oak-Hickory Habitat Types at Two Levels Using a YSI Telethermometer


Temperature (°C)
35
30
25
20
15
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25
Apr.
May
Jun.
Jul.
Aug.
Calendar Date
15.2 Cm
Soil Level
1972
15.2 Cm
Soil Level
1973

2

VITA

Allen Sterett Robertson

Candidate for the Degree of

Master of Science

Thesis: BEHAVIORAL OBSERVATIONS OF FED AND UNFED STAGES OF THE LONE STAR TICK, AMBLYOMMA AMERICANUM (LINNEAUS), IN RESPONSE TO VARIOUS ENVIRONMENTAL PARAMETERS

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