Reprinted from
THE JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
Volume 20, July, 1947, Number 3.

STUDIES ON THE BIOLOGY OF TRIATOMA SANGUISUGA (LECONTE) IN KANSAS, (REDUVIIDAE, HEMIPTERA)*[1]

ALBERT W. GRUNDEMANN
Department of Biology, University of Utah

This is an account of the bionomics of **Triatoma sanguisuga** (LeConte) based upon observations made in connection with studies in Kansas upon the transmission and reservoir of the virus of equine encephalomyelitis. It was discovered by Kitselman and Grundmann (1940) that this insect occurred in a naturally infected condition in the pastures and hillsides about Manhattan, Kansas. In order to more fully understand the relationship of **Triatoma** to this important neurotropic virus disease of man and the horse, and to aid in estimating its importance as reservoir and vector, it was found necessary to acquire additional knowledge concerning the life cycle and habits of this hematophagous species in the area.

Originally described by LeConte (1855) from Georgia and South Carolina, the species ranges as far north as southern Illinois, and from the Atlantic seaboard to Arizona, covering the entire southern part of the United States. It is also found in Mexico along the western seaboard to the latitude of the tip of lower California. A complete record of its range is reported by Usinger (1944).

Early references to the biology of **T. sanguisuga** are mostly in regard to its bloodsucking habits. LeConte (1855) reported that the insect could inflict a painful bite and was remarkable because it sucked the blood of mammals, preferring children in particular. Walsh and Riley (1869) also gained evidence that the insect was a seeker of human blood. Kimball (1894) stated that the insect was often found in her home and that it had increased in such numbers in the region of Manhattan, Kansas, that it was considered a common insect. She also observed the adults flying into stables and hen houses and feeding upon horses and chickens. Readio (1927) has summarized published work prior to his publication and reports Morrill as stating that in many parts of Arizona, **Triatoma** species have taken the place of the common bedbug as a household pest. More recent notes upon the distribution and habits may be found in publications by Wood (1940) and Usinger (1944).

Within the last few years, this species has been shown to be a potential menace to health. In addition to being naturally infected with western

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*Contribution No. 550 from the Department of Entomology, Kansas State College.
[1]This paper is an outgrowth of a study of the relationship of arthropods to equine encephalomyelitis at Kansas State College, which was financed in part by a grant from the Horse and Mule Associaiton of America. The facilities of the School of Veterinary Medicine and of the Department of Entomology of the Kansas State College of Agriculture and Applied Science were used in this study. The project was conducted under the supervision of Dr. Roger C. Smith, head, Department of Entomology, Dr. L. M. Roderick, head, Department of Veterinary Pathology, and Dr. C. H. Kitselman, Pathologist, Kansas Agricultural Experiment Station.

strain equine encephalomyelitis, it has been reported to be naturally infected with **Trypanosoma cruzi** of Chagas Disease as reported by Davis, McGregor and de Shazo (1943).

APPARATUS AND TECHNIQUE

Apparatus was developed for two purposes: First, to maintain cultures of the insect in the laboratory, and second, to maintain individual insects for life cycle observations. The apparatus developed for the first purpose consisted of two cages, a smaller one placed inside a larger. The larger cage was 18x18x24 inches and was constructed of wood and screen with one side removable as a tight fitting door. The inner, and smaller, cage containing the host animal used to provide blood for the colony was made up of two office letter baskets wired together hinge-fashion at one side with a wire fastening on the other side. The animal cage was held above the floor of the larger cage by being placed upon blocks of wood. Paper toweling placed beneath the animal cage caught the feces and absorbed the urine. In an attempt to simulate natural conditions, trash of various types, such as paper, sticks, stones etc., was placed in the outer cage to provide concealment for the specimens. The cages were kept darkened and a guinea pig or wood rat was placed in the inner cage overnight once every five days to provide the necessary blood. Moisture was provided by placing a moist piece of absorbent cotton in the cages daily.

Small ant cages and large vials served as containers used in the second or life cycle experiments. The ant cages obtained from Ward's Biological Supply were very good as they have a darkened section with excellent possibilities of observations. When vials were used, strips of paper toweling were included to give the insects something upon which to cling and to absorb excreta. Small pledgets of cotton were moistened daily and placed in the vials, since it was found that in case moisture was insufficient, molting would not be normal and the insect would be unable to cast completely the exuviae which usually proved fatal. Individual specimens were placed in contact with an animal overnight in the apparatus described for maintaining cultures in the laboratory.

When insects were fed upon horses, a screen cage was used which could be fastened to the shaven side of the animal with adhesive tape. Four or five specimens of different instars were allowed to feed at the same time. When monkeys were used, a cage was constructed which contained a false bottom. The specimens to be fed were placed in the bottom section which contained holes one-half inch in diameter to allow the specimens access to the cage containing the monkey.

The principal animals used for feeding purposes in the laboratory were guinea pigs and wood rats. In addition, horses and a rhesus monkey were used in a number of trials. Insects fed upon the blood of one animal did not hesitate to engorge when placed upon an animal of a different species for the next feeding, nor did the blood of the various species in subsequent feedings appear to affect development.

FIELD OBSERVATIONS

The natural host of T. sanguisuga in the region of Manhattan was found to be the wood rat, **Neotoma floridana baileyi** Merriam, and it was from the nests of this species that the majority of the specimens collected were taken. On several occasions, specimens were also taken from the nests of the western cotton rat, **Sigmodon hispidus texianus** (Audubon and Backman). The insect also feeds upon other animals in its environment, since a few of the specimens were collected at a distance from rodent burrows. On one occasion, three nymphs examined for virus were found to be engorged with a clear yellowish fluid resembling blood serum, possibly insect blood.

The wood rat host was found to build its burrows beneath the flat stones along the limestone outcrops protruding from many of the hillside pastures of eastern Kansas and abundant in the area about Manhattan. Outcrops near bushy and woody areas were found to be preferred by the rats since these localities provide more abundant food than the open grassy areas. In the valley bottoms, especially wooded sections where suitable stones were absent, the rat nests were built of detritus and sticks. Few of the latter type nests were found that were not built within a bush or about the base of a small tree, since some supporting structure is needed to keep the nest from easily being disturbed. Nests were also found in wood piles on the farms.

Most of the specimens taken were collected from nests built beneath loose stones along the limestone outcrops. These nests could be easily located by the sticks and detritus which the rats pile on top of the overlying stone and about the entrance to the nest beneath the stone. When the overlying stone was overturned, adults and nymphs could be found clinging to the underside or in the cracks and crevices of the stone, and in the detritus and small rocks within a yard of the inner nest of the rat. The insects apparently select resting positions that are well protected from the host.

The nests most commonly selected by the insects were those providing a more or less constant micro-climate and remaining dry throughout the year. The nests most heavily parasitized were those in which the overlying rock was found to rest upon a series of broken rock or talus as in an eroded bedding plane. This type provides a multitude of dry cracks and crevices into which the **Triatoma** could retreat while digesting their meals. Stones allowing water to drain beneath them during wet weather or embedded in the soil of the hillside were not selected by either the rats or the insects.

When the flat, overlying stones were overturned, many of the insects could be found clinging to the underside. The position, with the ventral side uppermost, seems to be preferred while the insects are digesting their meals. It was also prevalent in the laboratory colonies where they could hang on the underside of the animal cage, and other detritus provided for their concealment. The nymphs appear to be negatively phototropic at all times. The adults, become positively phototropic soon after molting and may be collected about lights in the vicinity. After fertilization, the adults find a host and do not use their wings again.

The insects were found to hibernate during the cold portions of the year. There is no diapause, since field observation showed them to become sluggishly active during warm winter days. Some nymphs appeared to overwinter in a partially engorged condition. During hibernation the insects assume a dorso-ventral position.

The results of the collections of T. sanguisuga are summarized in Table I. Specimens were sent to H. G. Barbour of the Bureau of Insect Identification and to Dr. A. Packchanian of the United States Public Health Service for verification, and to the latter for examination for infection with Trypanosoma cruzi. A total of 375 specimens were collected during the sur-

Table I. Summary of Triatoma sanguisuga collected for experimental purposes in the vicinity of Manhattan, Kansas, from May, 1940 to November, 1941.

	Instar.											
Date	1	2	3	4	5	6	7	8	M	F	*	**
May 12, 1940	....	....	....	....	4	1	4	....	2	3	14	28
May 28, 1940	....	....	....	2	....	5	7	....	2	2	17	28
June 11, 1940	....	....	....	4	5	....	3	3	1	3	19	26.3
June 21, 1940	....	....	....	....	....	3	4	....	3	4	14	28.5
June 28, 1940	....	2	1	4	3	1	3	....	....	1	15	40
Aug. 10, 1940	....	3	4	....	....	....	....	5	2	4	18	22.2
Nov. 29, 1940	....	....	1	1	1	1	8	....	2	....	14	14.2
Jan. 11, 1941	....	2	4	6	4	3	4	2	....	....	25	4
Feb. 17, 1941	....	....	....	....	....	....	....	1	1	1	3	0
Mar. 11, 1941	....	....	....	....	....	....	....	....	....	....	0	0
Apr. 10, 1941	....	....	....	1	....	....	1	....	....	....	2	0
Apr. 11, 1941	....	....	....	....	....	....	....	....	1	....	1	0
Apr. 12, 1941	....	....	1	....	1	....	....	....	....	....	2	0
Apr. 17, 1941	....	....	....	1	....	....	....	1	....	....	2	0
Apr. 22, 1941	....	3	4	1	....	1	2	....	....	....	11	20
Apr. 24, 1941	....	3	3	1	4	4	2	6	....	....	23	43.4
May 6, 1941	....	2	1	....	....	1	2	....	....	....	6	16.6
May 8, 1941	....	1	2	3	3	5	5	2	....	....	21	38
May 13, 1941	....	6	4	5	4	7	9	7	1	1	44	47.7
June 5, 1941	2	6	3	3	2	4	3	4	1	3	31	37
July 8, 1941	1	....	3	2	5	1	....	3	1	2	18	22
Sept. 11, 1941	1	5	4	3	3	3	5	7	1	3	35	18.1
Oct. 13, 1941	1	5	4	1	1	5	3	1	1	....	22	14.2
Nov. 11, 1941	....	8	2	1	....	2	....	3	....	....	18	16.6
Totals	5	46	41	39	40	47	65	45	19	27	375	

*Total number insects collected.

**Percent naturally engorged.

vey, which covered a period of eighteen months. A more or less equal distribution was noted among the various instars, with the exception of the first instar, a number of which were probably overlooked, and the adults, some of which had migrated previously.

Some wood rat nests were very heavily infested while some were entirely free from parasites. One nest investigated contained 23 Triatoma of various instars, 77 Ornithodoros turicata Duges and seven fleas, Epitedia wenmanni (Roths).

LABORATORY OBSERVATIONS

Life Cycle Studies. The egg of T. sanguisuga is about 1.5 mm. in length, oval, and pearly-white in color. There is an operculum at one end which is forced off during eclosion. The embryo is encased in its embryonic membrane, from which it emerges, leaving the membrane attached to the shell. The eggs are deposited singly and indiscriminately without apparent regard for micro-climate. There is no adhesive material to fasten them to a surface. In nature, the eggs, are deposited while the female is quiescently digesting the blood meal.

Temperature was found to have an effect upon both oviposition and embryonic development. One to three eggs were deposited daily when the mean daily temperature was below 80 degrees F. and three to five daily when above. Embryonic development was accelerated by increased temperatures and retarded by lowered temperatures. Eggs were found to hatch in 13 to 32 days when the mean daily temperature was 80 degrees F. in May and early June, and 13 to 23 days during July and August when mean temperatures were above 80 degrees. Humidity apparently has little effect upon the speed of development or upon oviposition. This corroborates the results obtained by Clark (1935) who demonstrated that low temperatures retard and high temperatures accelerate development in Rhodnius prolixus Stal., a closely related species, while a normal humidity range has little effect.

Upon dissecting newly-molted females, it was found that seven to fifteen eggs are matured in the ovarioles. These are normally not deposited until the female has been fertilized and obtained a blood meal. Oviposition began four to six days following a blood meal and one to five eggs were deposited daily, depending upon the temperature, until the ovarioles were empty. The female then matures a second group which are not deposited normally until after the next blood meal. In several cases observed, females that were prevented from fertilization retained the initial group of eggs in the body until death.

From six to eight days prior to hatching, the egg turns pinkish, the color becoming more intense the closer the embryo approaches eclosion. This color change apparently is caused by the chorion which allows the embryo color to show through.

In nature the eggs are laid beginning in May and ceasing about the middle of September.

Fertilization and Blood Meals. The newly-molted adults migrate from the wood rat nests for fertilization. They become positively phototropic at this time, use their wings, and may be collected about lights in nearby areas. One fertilization apparently lasts the female throughout her life. Once the female has been fertilized, she finds a host, engorges, and begins the establishment of a colony.

During the 24 hour period following engorgement, **T. sanguisuga** eliminates a considerable quantity of liquid fecal material. This initial elimination consists of the excess water taken in with the engorged blood, and the residue of metabolism remaining in the Malphigian tubules from the last engorgement. Later excretions consist of a meconium of darker material which contains considerable quantities of hemoglobin and very little moisture. At the completion of engorgement, the insects were observed to defecate the contents of the fecal pouch, a function characteristic of the genus. The above observations are similar to those of Wigglesworth (1931) in his studies of **Rhodnius prolixus** Stal.

Hosts. The female, following fertilization, seeks a meal of blood from some source, preferably a mammal. In most cases, it enters the burrows of its normal host which in this region was found to be a wood rat, **Neotoma floridana baileyi** Merriam. The species is by no means host specific, either in the laboratory or in the field; specimens were observed to enter stables and feed upon horses and chickens, and go into homes where in several cases both nymphs and adults were taken engorged from the beds of inmates. In the field, they were taken from the burrows of the western cotton rat, **Sigmodon hispidus texianus** (Audubon and Backman), and in all probability feed upon other rodents and animals present in the environment. In the laboratory there was no difficulty in obtaining feedings upon guinea pigs, horses and mules, the rhesus monkey, and man.

The Nymphal Instars. Through laboratory rearing and by measurement of the head capsules of nymphs, **T. sanguisuga** was found to have eight nymphal instars. The overall size of the insect proved to be a very poor criterion for determining the instar, since the abdomens may be in various stages of distension with blood and distort the proportions. A more satisfactory means of determining the instar was through the measurement of the head capsule immediately posterior to the eyes. Measurement of the head capsules of dried specimens showed that the increment of size was approximately 0.1 mm. per instar. Results of the measurement appear in the following table.

Length of the Life Cycle. The life cycle was found to be about 450 days in laboratory rearings. Estimates of the length of the cycle in nature were made upon the basis of the average length of instar, the length of adult life, and the length of the active season in this region. These cycles were calculated to be considerably longer than the cycle in the laboratory which makes no allowance for seasonal activity.

The average length of instars in laboratory (and seasonal rearing) was found to be approximately 41 days. No appreciable difference in length

Table II Width of the head capsule of dried specimens in millimeters

Instar	Greatest	Least	Averages
First	0.431	0.425	0.428
Second	0.536	0.534	0.535
Third	0.653	0.620	0.642
Fourth	0.750	0.719	0.738
Fifth	0.872	0.856	0.864
Sixth	0.963	0.948	0.956
Seventh	1.071	1.071	1.071
Eighth	1.193	1.147	1.168
Adult	1.078	1.068	1.071

of instar was noted between the earlier instars and the later ones. Seventy-five per cent of the nymphs molted following a single engorgement and are designated as Group I. The remainder, except two, molted following two engorgements and are designated as Group II. These engorgements were made in the apparatus described previously for maintaining the colonies in the laboratory and approached natural conditions where the insects have access to an animal that is capable of movement. The insects that failed to molt following a single engorgement are considered to be those that were disturbed during feeding, thereby not becoming fully engorged; since full engorgement is considered necessary to stimulate the molting hormones, (Wigglesworth, 1933), this group failed to molt and so required a second engorgement.

Group I averaged 36 days as the length of instar. During May and June, the average time was 40 days. When mean daily temperatures were higher during July and August, the period was shortened to 28 days. The average time between feedings in Group II was found to be 29 days during May and June and 26 days during July and August, with an average of 55 days between molts. Thus compiling the figures for both groups would give an average length of instar of 41 days.

The adults of T. sanguisuga are long lived. Wood (1941) reported that a female of this species lived 155 days on four feedings. In the present observations a female lived 81 days on three feedings of guinea pig blood, and another lived 102 days on three feedings. Last instar nymphs were found to molt to adults at Manhattan from May 1 to about October 15. Those molting late in the season appeared to remain in the nests until the following spring and constituted a portion of the adults found in the nests during the winter. Other adults, being long-lived, lived over from one season to the next.

The active season in the region of Manhattan appeared to be between 200 and 235 days per year, or from about March 15 to November 15. Although the insects may be active after March 15, they apparently do not engorge until about April 15, as shown in Table I. In a normal year it is doubtful if any engorgement takes place after October 30, though on warm days the temperature may be high enough; but at night the temperatures would be such as to inactivate the insects. The season during which molting takes place is estimated as approximately 200 days.

The life cycle estimate of 450 days in the laboratory depends upon the availability of hosts and the relatively constant temperatures which do not occur in nature. In favorable seasons, four to five instars may occur each season. All instars except the first may be found in the wood rat nests at any time of the year, as may be seen by reference to Table I. Since the females lay eggs at intervals throughout their lives, a great complexity in nest composition becomes inevitable. Thus, a first instar arising in May when the first series of eggs are hatched would undergo three instars the first summer, over-winter as a third instar nymph, pass four or five instars the second summer, and over-winter as an eighth instar nymph. This individual would molt to an adult in the spring and pass the third season as adult, and might even pass the third winter in the adult stage. The life cycle as based upon this example would cover approximately three years, making the Triatoma an excellent reservoir for infection.

Sex Ratio. Field collections, as shown in Table I, show that approximately 41 per cent of all adults collected were males, while the laboratory rearings of 16 eighth-instar nymphs to adults gave approximately 32 per cent males. On the basis of collections and rearings, it is evident that there are more females than males, but the exact ratio has not been determined.

Feeding Observations. Triatoma when hungry were found to feed readily upon mammals of several species. To check the details of engorgement, the author allowed a number of laboratory-reared Triatoma to feed upon the back of the hand. The bite of the insect was found to be somewhat anesthetic, since the host does not become disturbed during the feeding process lasting from three to eight minutes. The only indication of the presence of the insect was a slight tickling sensation when the proboscis was first introduced, and no reaction followed the bites. However, severe reactions have been observed and reported from several individuals sensitive to the bites of this species.

Feedings occurs only during the dark hours of the day or under darkened conditions. Insects were fed upon horses between the hours of 8 and 10 p.m. They were left in contact with the animal for a period of 20 minutes in a specially prepared screen cage that was taped to the side of the animal. Those insects in a physiological state of hunger fed readily, and those not in this condition could not be induced to feed under any conditions.

SUMMARY

1. T. sanguisuga was calculated to have a life cycle of approximately three years under natural conditions in Kansas, with eight nymphal instars and an adult stage.

2. The natural host in this region was found to be the wood rat Neotoma floridana baileyi Merriam, which is the common wood rat of the region

found in the pastures along the hillsides. The western cotton rat, **Sigmodon hispidus texianus** (Audubon and Backman) serves as an occasional host. So do other animals living in the environment.

3. The adult female is long-lived and lays a group of eggs following each blood meal. Temperature affects the development of the insect and of its eggs, in that high temperature accelerates and low temperature retards the development. Humidity does not appear to affect the development except as regards molting, and high humidity is generally avoided by the insect in its normal environment.

4. The life cycle of three years duration could make the insect important as a reservoir host of equine encephalomyelitis virus; coupled with the fact that the insect will feed upon almost any animal, this could make it one of the important factors in the maintenance of the disease among rodents and wildlife in the region of eastern Kansas.

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