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BIONOMICS OF *SABETHES CHLOROPTERUS* HUMBOLDT, A VECTOR OF SYLVAN YELLOW FEVER IN MIDDLE AMERICA[1]

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INTRODUCTION

Shannon *et al.*, (1938) first called attention to the sabethine mosquitoes as possible vectors of yellow fever when they isolated the virus by injecting into mice a mixed pool of 88 wild-caught specimens of *Sabethoides, Limatus, Wyeomyia* and *Trichoprosopon*. The staff of the Rockefeller Foundation in Brazil later did a considerable amount of largely unpublished work with sabethine mosquitoes and yellow fever virus, mostly with negative or unsatisfactory results (Strode, 1951). Galindo *et al.*, (1950, 1951) and Trapido and Galindo (1956, 1957) based on epidemiological evidence, focused attention on *Sabethes chloropterus* as a vector of sylvan yellow fever in Middle America. Galindo *et al.*, (1956) transmitted yellow fever from monkey to monkey by the bite of *S. chloropterus* and Rodaniche and Galindo (1957) and Rodaniche, Galindo and Johnson (1957) isolated the virus from wild-caught females of this species in Panama and Guatemala.

The interest of this Laboratory in *Sabethes chloropterus* dates back to the first investigations on yellow fever carried out in Panama during the year 1949. Since then much time and effort have been spent in attempting to establish a laboratory colony and in acquiring basic information on the biology of this species which could be applied to advantage in transmission experiments with yellow fever virus. The results of these investigations are presented in this publication as a preliminary note, which may form the basis for future work on this and other species of the tribe Sabethini.

ESTABLISHMENT OF A LABORATORY COLONY

The colony was started from large numbers of adults reared from eggs obtained from females captured in the Cerro Azul area of Panama by the method described by Galindo *et al.*, (1950). Freshly emerged males and females were placed in 1-meter cubical screened cages. The lower half of one of the sides of each cage had a large opening covered with a cloth sleeve and a sliding panel, through which objects could be taken in and out. A glass pane on the upper half of this side of the cage permitted close observation of the colony. The remaining sides and top were completely lined with thick muslin cloth carefully machine-sewn and taped to the edges to prevent trapping of mosquitoes between the cloth and the screen. The muslin served the dual purpose of helping to maintain favorable humidity inside the cage and of allowing quick detection of such pests as cockroaches, spiders or mites, which might invade the colony. A thick layer of wet cotton placed on top and a large pan of water covered with cheese cloth inside the cage served to maintain adequate humidity for the colony. During the dry season the colony room was tightly sealed and the temperature and humidity were regulated by means of a large electrical humidifier. In this manner the colony was maintained at temperatures which fluctuated between 23°C and 30°C and relative humidities between 70 and 100 per cent.

Females were allowed to feed on blood by exposing to their bites a trussed rhesus monkey or a guinea pig every day, except Sundays and holidays, from hour 0900 to midday. Sugar solution was available to the mosquitoes in the form of a soaked cotton ball hung from the top of the cage and changed daily.

In order to simulate closely the natural breeding sites of the species (Galindo *et al.*, 1951), a well-ripened section of bamboo about 4 inches in diameter, half filled with water, was used as an oviposition receptacle. The top of the bamboo was closed with a lid, and a hole 1 inch in diameter was drilled through the side. Eggs were removed from the bamboo every other day by pouring the water into a small enamel pan.

As the larvae hatched they were transferred to large pans and reared in a yeast-infusion medium. Because of the cannibalistic habits of the larvae discussed below, only specimens of the same

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instar were kept in one pan. Pupae were removed daily and placed in small finger bowls under a lamp chimney for emergence. Adult specimens were transferred to the colony cage from 12 to 24 hours after emergence. The colony has thrived under these conditions and has been maintained in our laboratory for over 2 years.

BITING HABITS

As pointed out by Galindo *et al.*, (1950, 1951) *S. chloropterus* is strictly diurnal in habits. In long-term observations carried out in Panama by Trapido and Galindo (Galindo *et al.*, 1950; Trapido and Galindo, 1957), it has been demon-

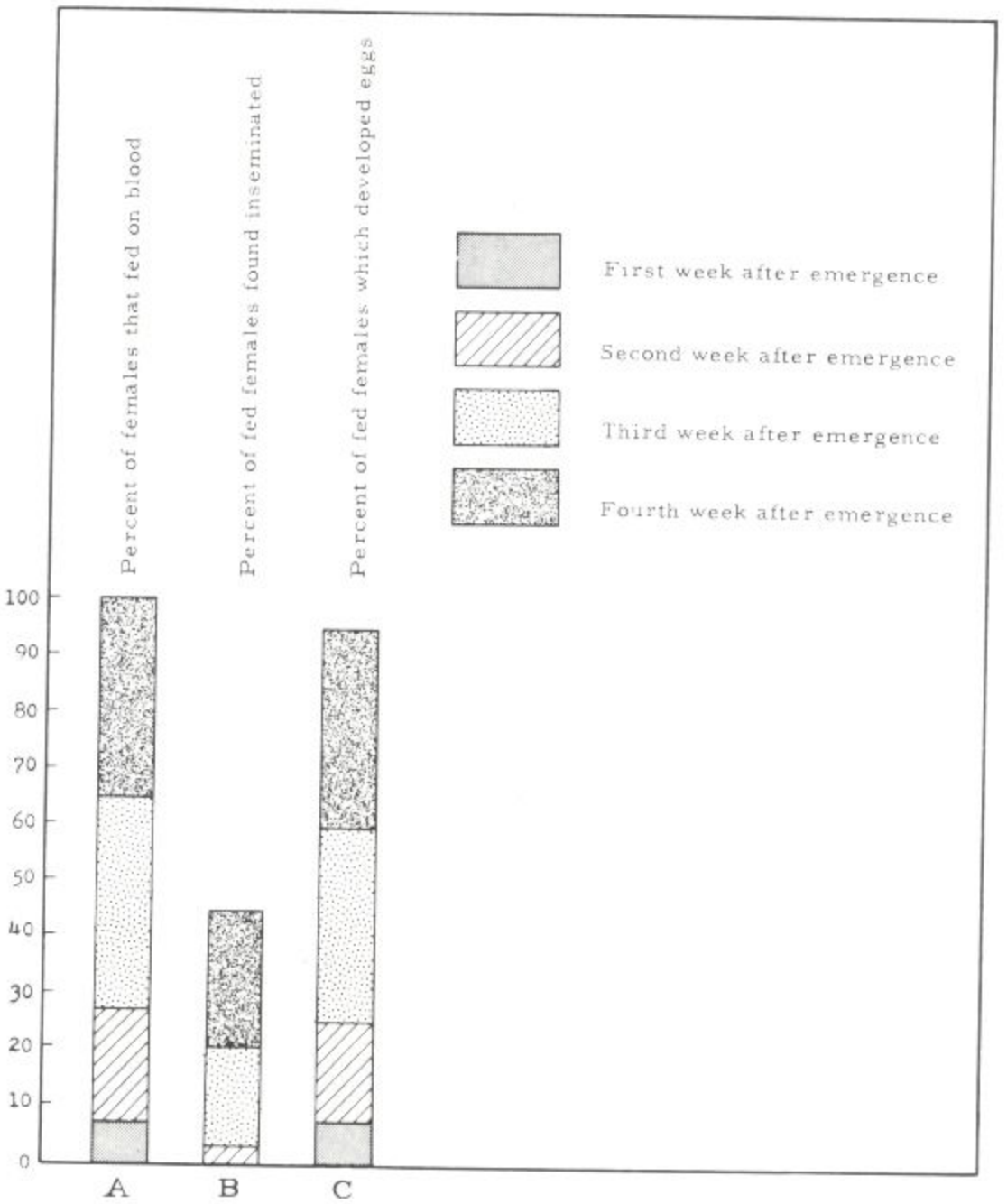

FIG. 1

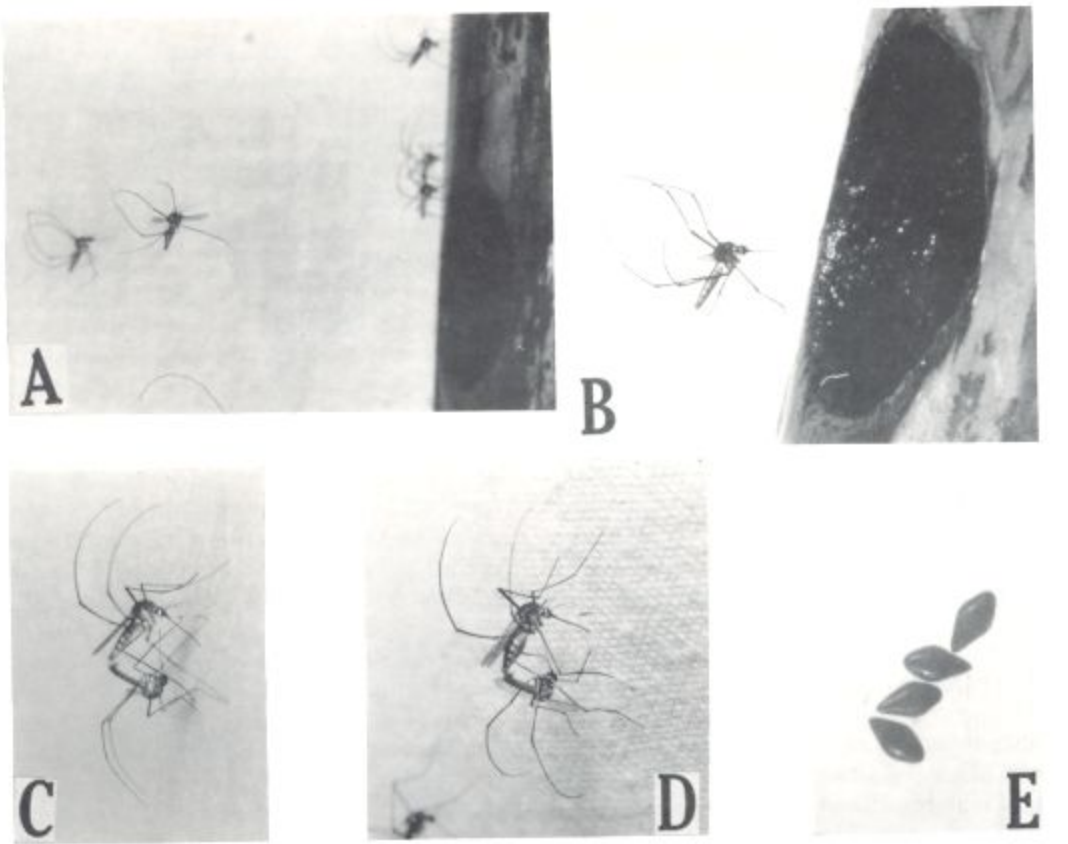

PLATE 1

FIGS. A and B.—*S. chloropterus* females hovering in front of entrance hole, thrusting eggs into a bamboo pot half filled with water. FIGS. C and D.—*S. chloropterus* in the act of mating. FIG. E.—Eggs of *S. chloropterus*.

strated that this mosquito shows a daily biting cycle common to many neotropical diurnal forest mosquitoes, seeking a blood meal in greatest numbers during the early afternoon hours (1400-1500). This, in turn, corresponds to the midday rest period of most of the arboreal forest mammals which serve as hosts for this species.

In the laboratory, both males and females become engorged on sugar solution from 6 to 24 hours after emergence. No female has been observed feeding on blood before the fifth day after emergence. The peak of biting activity does not occur until the second or third week and it may be as long as 30 days before most females of a particular brood take a blood meal. Figure 1, column A, shows the results of an experiment in which 40 females emerging on June 3, were permitted to feed on a rhesus monkey every day from hour 0900 to 1200. These females were kept in a regular cage together with some 50 males and were treated in the same manner as the stock colony. On the fifth day after emergence the first female became engorged with blood, and by the end of the first week only 7.5 per cent had taken blood. At the end of the second week 27.5 per cent of the females had engorged, while at the end of the third week 65 per cent had bitten the monkey. This delay in taking the first blood meal had caused considerable trouble in transmission experiments on yellow fever with this species since freshly emerged females, which are usually employed in this type of work, invariably refuse to bite. Our practice now is to use for these experiments females that have previously fed on blood or those that show willingness to attack an animal introduced in the cage. This practice of using older females for transmission is feasible in this particular species since, as will be seen later, the mean life span of *S. chloropterus* is considerably longer than the normal extrinsic incubation

period of yellow fever. Females of *S. chloropterus* prefer to bite high on the body, having a special predilection for the nose and lips.

MATING

S. chloropterus is a stenogamic species; that is to say, it is capable of mating in a small, confined space. Coupling of the sexes occurs while resting on a surface and it is preceded by peculiar epigamic activity on the part of the males. (See Plate I.) A male approaches a female from one side and with the mid-tarsus lightly taps the opposite hind leg of the female. It then hovers to the other side and goes through the same motion. This is repeated several times until the male suddenly pulls forward the mid-tarsus closest to the female, twists its body upside down and with a sliding motion attempts to drop directly under the female by seizing the surface of the wall with the fore-legs. The males usually overshoot their mark, in which case they may come back to start the epigamic motions all over again, fly to another female, or come to rest on the wall. If a male manages to get a hold on the wall, it immediately bends its abdomen upward and forward until it comes in contact with the tip of the female's abdomen and copulation begins. In 35 instances in which the time was measured, mating lasted from 14 seconds to 34 minutes, with an average of 6 minutes. During copulation the female remains motionless while the mid-tarsi of the male quiver rapidly, lightly tapping the tips of the female's antennae.

Copulation in this sabethine mosquito has not been observed before the sixth day after emergence and the peak of mating activity is not usually reached before the second or third week of the female's life. Columns B and C of Figure 1 show the results of an experiment in which 40 females kept in a colony together with 50 males were given the opportunity to feed daily on a rhesus monkey. Those females which engorged on blood were removed from the cage, held in separate vials for 6 days and then dissected to determine the rate of insemination and the number of specimens with fully developed ovaries. As can be observed, insemination does not necessarily occur before the first blood meal, and does not appear to be essential for ovarian development, since only 45 per cent of the females were found to be inseminated, while 95 per cent of the specimens showed full ovarian development.

OVIPOSITION

The author (Galindo, 1957) has recently described the laboratory behavior of *S. chloropterus* while ovipositing in a bamboo internode with closed top and a 1-inch hole on the side, in the following manner: The female when ready to oviposit, approaches the bamboo in the characteristic slow flight peculiar to the genus and usualy flies around it two or three times probing here and there until the entrance hole is found. (See Plate I.) Once this is accomplished, the female hovers outside and in front of the opening at a distance of from a few mm to as much as 5 cm, with the fore and hind tarsi almost locked together above the thorax and the mid-legs extended downward and outward. After hovering for a variable length of time, and while still in flight, the mosquito suddenly jerks the head and thorax back and thrusts the abdomen forward, forcibly ejecting at the same time one or two eggs which shoot through the entrance hole and into the water in the cavity. Almost in the same movement the female darts back rapidly a few cm and then resumes normal flight. The entire process takes place with incredible speed and is completed in but fractions of a second. A female which has just laid may come back immediately

TABLE 1

Rate of oviposition in S. chloropterus *during the different hours of the day*

Hour	0600 to 0700	0700 to 0800	0800 to 0900	0900 to 1000	1000 to 1100	1100 to 1200	1200 to 1300	1300 to 1400	1400 to 1500	1500 to 1600	1600 to 1700	1700 to 1800	1800 to 0600
Aver. light intensity in ft. candles	2.2	3.1	3.5	3.7	3.6	3.8	3.9	3.6	2.9	2.2	1.1	0.2	—
No. of eggs	191	312	397	576	449	630	855	670	990	603	584	280	0
Per cent of total	2.9	4.8	6.1	8.8	6.9	9.6	13.1	10.2	15.1	9.2	8.9	4.4	0

TABLE 2

Rate of oviposition of S. chloropterus *females during four periods of the day*

Period of the day	Early morning 0600–0900	Late morning 0900–1200	Early afternoon 1200–1500	Late afternoon 1500–1800
No. of eggs	900	1,655	2,515	1,467
Per cent of total	13.8	25.3	38.5	22.4

and go through the same motions for as many as eighteen consecutive times, or it may alight on the bamboo or some other surface nearby, only to resume egg-laying after resting for a few minutes. Tables 1 and 2 give the overall results of a series of experiments carried out during different seasons of the year, by which we determined the peak hours during which 6,537 eggs of *S. chloropterus* were laid.

As can be observed in Table 1, no eggs were laid in the total absence of light during hours 1800 to 0600. However, the position of the sun in the sky rather than light intensity seems to be the determining factor in inducing oviposition in this species. In our insectary cages light intensity is greatest in the morning, while the largest number of eggs were laid in the afternoon. In Table 2 the daylight hours are divided into four periods: early morning (0600–0900), late morning (0900–1200), early afternoon (1200–1500) and late afternoon (1500–1800). The greatest percentage of eggs (38.5%) were laid during early afternoon, while only slightly fewer eggs (22.4%) were deposited in late afternoon than in late morning (25.3%). The smallest number of eggs (13.8%) were laid during the early morning period. This peak of egg-laying activity during early afternoon also corresponds with the period of the day when the greatest number of females seek a blood meal.

S. chloropterus is a nonautogenous species; that is to say, it must have a blood meal (or its equivalent in certain proteins) before egg-laying takes place. As was pointed out when mating was discussed, copulation is not usually necessary to induce ovarian development, but a small percentage of virgin females fail to produce eggs even after fully engorging with blood several times. It must be borne in mind, however, that in some species of mosquitoes, such as *Aedes aegypti*, there is considerable variation of this physiological characteristic between local strains of the same species.

Table 3 and Figure 2 show the results of experiments made to determine egg production by day by *S. chloropterus* after a single blood meal. In these experiments, a stock colony was deprived of a blood meal until no eggs were laid for 10 consecutive days. A trussed monkey was then placed inside the cage and the fully engorged females were then collected and isolated individually in Barraud cages of 1 cubic foot, provided with bamboo sections about 1.5 inches in diameter, for oviposition. The water in the bamboos was examined daily for eggs during 15 days. As can be observed in Figure 2 oviposition began on the third day after the blood meal and went on through the thirteenth day. Most females oviposited during the fifth day. Table 3 indicates that, of 101 females which fully engorged with blood and which lived through the 15 days, 86 went on to lay a total of 3,323 eggs or 38.6 eggs

TABLE 3

Egg production by day in S. chloropterus *after a single blood meal*

Exp. No.	No. of females	No. of females which laid	Days after blood meal													Total eggs
			1	2	3	4	5	6	7	8	9	10	11	12	13	
1	15	10	0	0	0	18	90	348	22	9	1	13	6	6	0	522
2	13	13	0	0	0	42	196	173	28	18	11	3	3	0	0	474
3	14	12	0	0	0	25	27	45	62	34	1	8	8	9	1	220
4	17	17	0	0	0	23	89	196	132	118	3	0	0	0	0	561
5	20	13	0	0	8	23	116	101	116	45	27	28	0	0	0	464
6	17	17	0	0	43	186	215	347	33	39	9	0	0	0	0	872
7	4	4	0	0	0	132	44	24	10	0	0	0	0	0	0	210
Total	100	86	0	0	51	449	786	1234	403	263	52	52	17	15	1	3323

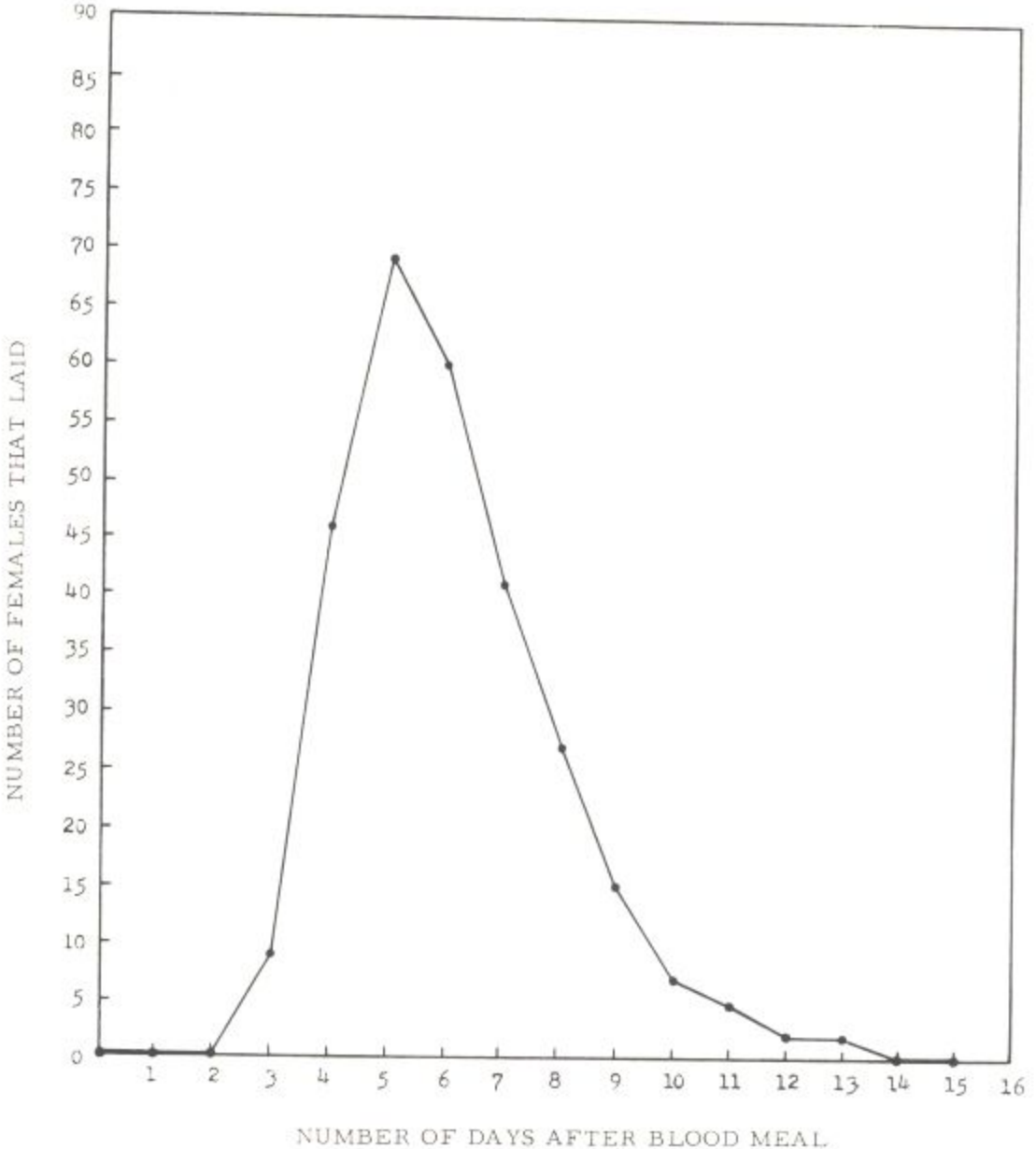

FIG. 2

per female. This table also shows that by far the the greatest number of eggs were laid during the sixth day, despite the fact that more females oviposited during the fifth day.

Experiments are still in progress to study the factors which determine the production of eggs, but it appears that, as in other species of mosquitoes, the size of the blood meal bears a direct relationship to the number of eggs produced. There are indications also that older females that have become blood-engorged several times tend to lay more eggs than those that have had but a single blood meal.

From the data presented in Table 3 it may be calculated that each female lays an average of 38.6 eggs every ovulation cycle and that one of these cycles is completed at colony-room temperatures every 11 days. If, as will be shown later, the mean life span after the initial blood meal of *S. chloropterus* females at these tempera-

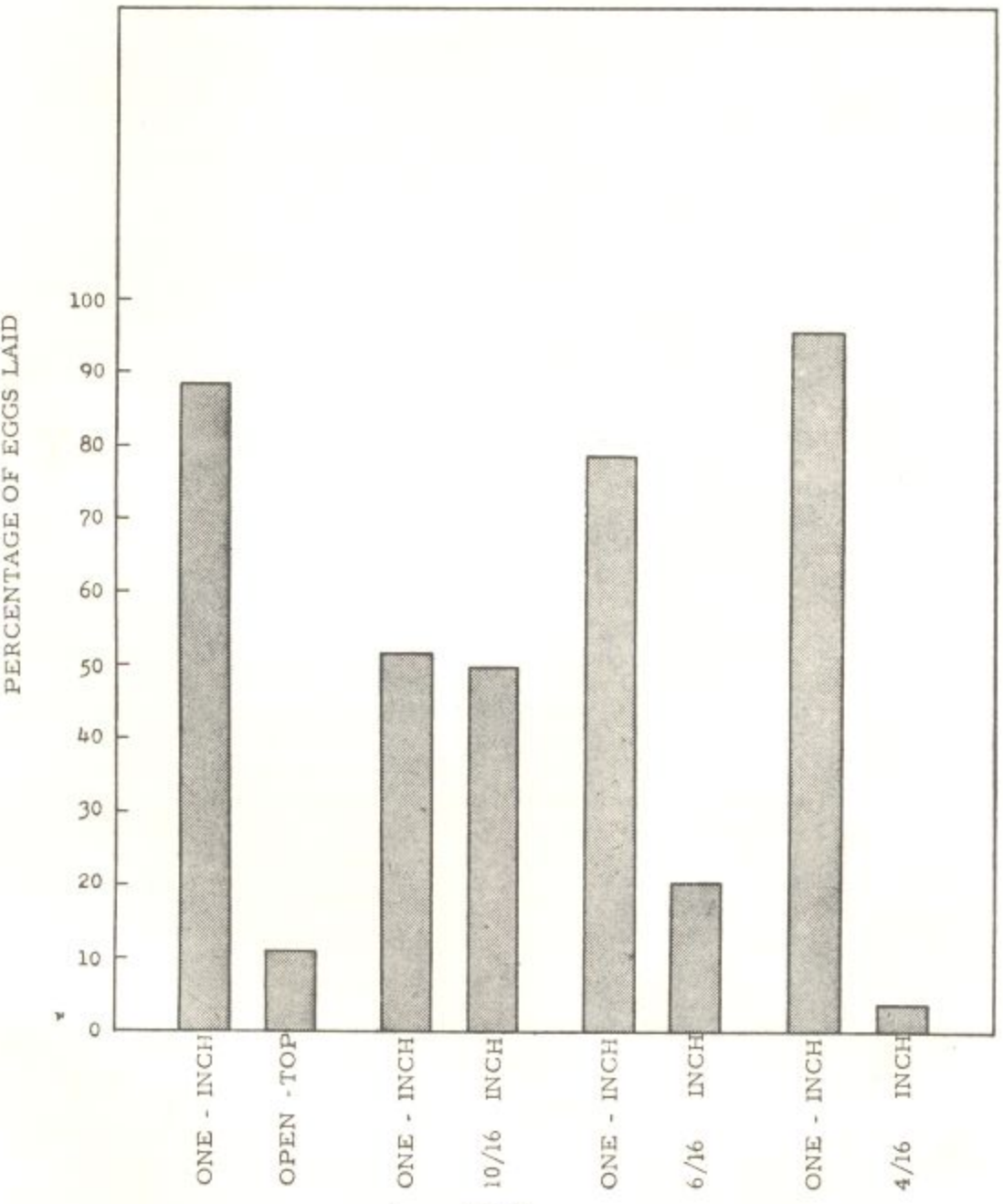

FIG. 3

tures is 38.9 days, then it would indicate that each female that survives through the first blood meal lays an average of 136.5 eggs during her life-time.

In order to check these figures, an experiment was made with three subcolonies totalling 382 females, in which we noted the total output of eggs from the initial blood meal until the last female died. It was found that these specimens laid 52,722 eggs or an average of 138.0 eggs per female, which checks very closely with the figure given above.

In Figure 3 are plotted the results of experiments set up to investigate the selection exercised

by *S. chloropterus* females when ovipositing in bamboos with different types of apertures. In the first of these experiments a bamboo with open top was placed inside a colony cage, together with a bamboo with closed top and a hole 1 inch in diameter drilled through the side. Eggs were removed daily from each bamboo and counted. The two bamboo pots were changed as to orientation and position every day, to avoid possible errors due to preference of the females for a particular spot in the cage. In the other experiments the same procedure was repeated but the open-top bamboo was eliminated and one with a 1-inch hole was paired with others having openings of 1 9/16 inch, 9/16 inch and 4/16 inch.

In the first experiment, of 5,129 eggs laid, 4,579 (89.3%) were deposited in the bamboo with closed top and 1-inch hole, while only 550 (10.7%) were found in the bamboo pot with open top. In the second experiment, of a total of 13,063 eggs, 6,551 (50.1%) were laid in the bamboo with a 1-inch hole and 6,512 (49.9%) in the section with a hole 1 9/16 inch in diameter. In the third experiment, a total of 6,832 eggs were laid, 5,392 (78.9%) being found in the bamboo with the 1-inch hole and 1,440 (21.1%) in the pot with the 9/16-inch hole. In the last experiment, of a total of 5,589 eggs, 5,367 (96.0%) were laid in the bamboo with a 1-inch hole and only 222 (4.0%) were deposited in the pot with the 4/16-inch hole. This preference for oviposition in a pot with a small lateral hole rather than in a section with open top is in agreement with the type of breeding place preferred by this species in nature, which consists of rot-holes with a large cavity and a small opening. Females do not appear to exercise any preference as between two bamboos having apertures of 1 inch and 1 9/16 inch, respectively. As the smaller of these apertures is decreased to 9/16 inch and 4/16 inch there is a definite predilection for egg-laying in the bamboo with the 1-inch opening.

THE EGG STAGE

The eggs of *S. chloropterus* are peculiarly rhomboid in shape, thus differing markedly from the known eggs of members of the tribe Culicini. (See Plate I.) It is interesting to note that eggs of this species are very similar to those of at least two species of typical *Sabethes*, namely, *S. cyaneus* and *S. tarsopus*, as well as to those of several species of *Wyeomyia*. However, they are strikingly different from the known eggs of *Trichoprosopon* (*digitatum, compressum, longipes, magnus*, etc), thus corroborating the close affinity that exists between *Wyeomyia* and *Sabethes*, through such an intermediate group as the subgenus *Davismyia*, and the wide divergence which evidently exists between these two genera and the more primitive sabethine genus *Trichoprosopon*.

The development of the embryo in *S. chloropterus* takes place somewhat more slowly than in most other mosquitoes, lasting from 3 to 4 days, but the eggs hatch soon after the larvae attain full development and are not capable of going into the prolonged diapause characteristic of some aedine species. In one experiment in which the time required for hatching 781 fertile eggs of *S. chloropterus* was recorded, the following results were obtained: 79.4 per cent of the eggs hatched on the third day after being laid, 18.4 per cent on the fourth, 0.9 per cent on the fifth, 1.2 per cent on the sixth and 0.1 per cent on the seventh day. The eggs of *S. chloropterus* are laid on the water surface and they may either float or sink to the bottom of the container, but there does not appear to be any difference in hatching response between the eggs on top or on the bottom. Eggs may be maintained for a few days on wet filter paper but they shrivel and die as soon as the paper becomes dry, while the larvae hatch in 6 or 7 days if kept moist. Eggs of this species can be successfully transported on journeys lasting no more than 6 days, by placing the eggs, soon after being laid, in Petri dishes containing wet cotton and lined with filter paper.

THE LARVAL STAGE

Despite the fact that the larvae of *S. chloropterus* live in very dark tree-holes with a small opening to the outside, they do not show any signs of being negatively phototropic and become evenly distributed when reared in well-lighted pans. These larvae, as those of many other sabethine species, are facultatively predaceous and will feed voraciously on other mosquito larvae if given the opportunity. The author has observed this species preying on the following mosquito larvae in the laboratory: *Anopheles albimanus, Haemagogus equinus, H. lucifer, Culex quinquefasciatus* and *Wyeomyia scotinomus*.

The larvae of *S. chloropterus* are also definitely cannibalistic and will prey on smaller larvae of their own species. In spite of this marked cannibalistic habit, larvae can be reared successfully

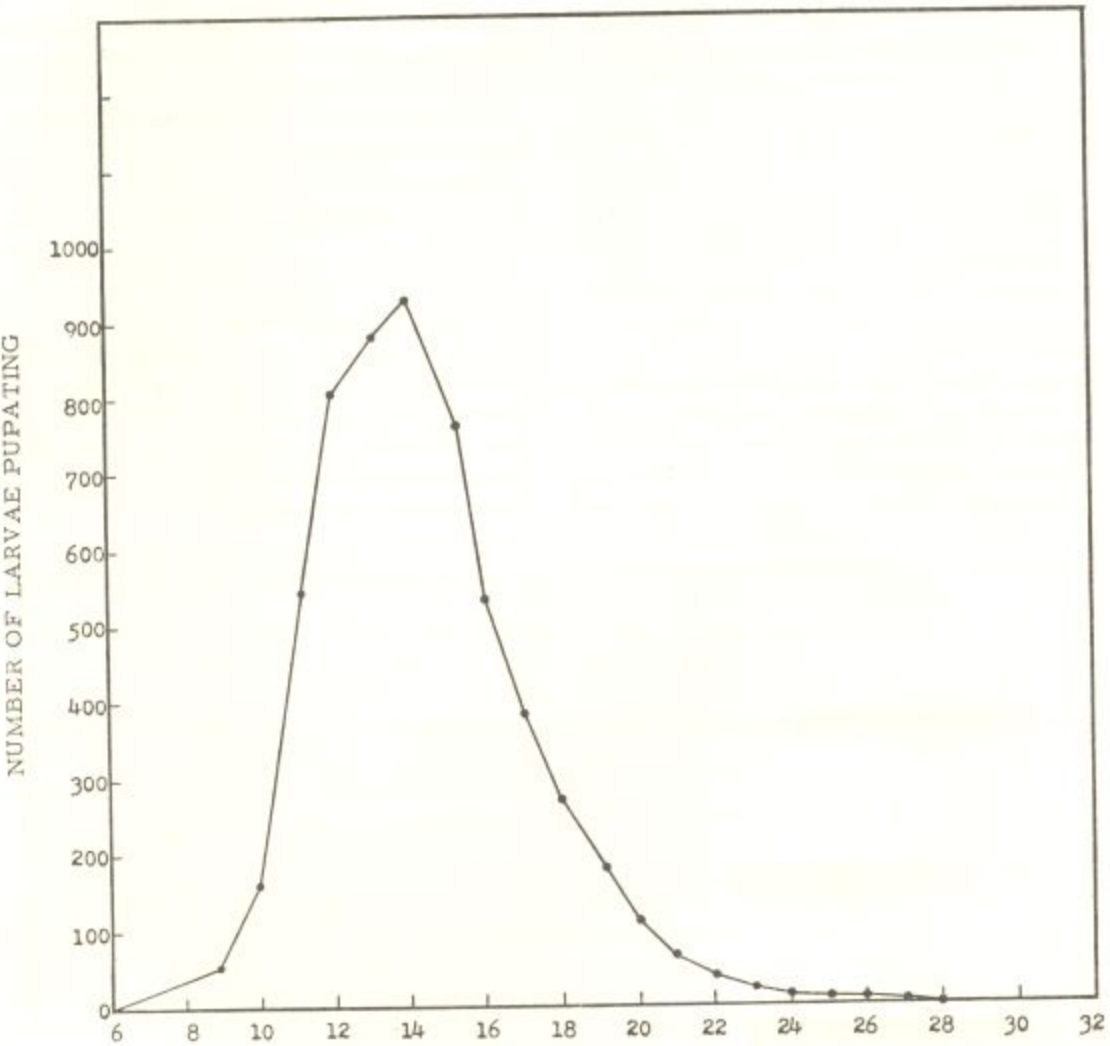

FIG. 4

in a yeast-infusion medium, provided that only specimens of the same instar are kept together. Even under these conditions a good number of larvae will attack and kill each other. This may be demonstrated by the fact that of over 32,000 larvae hatched and reared in our laboratory, in which the numbers of pupae were carefully counted, only 58.7 per cent reached the pupal stage. Galindo *et al.*, (1951) point out that predaceous sabethine larvae in general, and those of *S. chloropterus* in particular, do not swallow their prey but seize and puncture the cuticle with their hooked maxillae. Through this puncture and with the help of the mandibles, they gradually suck out the body contents of the victim and later drop the remains to the bottom of the container.

Figure 4 shows the overall results of a series of breeding experiments in which the rate of development of a total of 5,788 larvae was noted. These experiments were run at a mean bihourly temperature of the larval medium of 26°C, with a minimum of 24°C and a maximum of 30°C. The mean development period of these larvae from hatching to pupation was 14.8 days, with a maximum of 28 days and a minimum of 9 days. As would be expected, the rate of development depends a great deal on temperature and larval food. Larvae of this species have been observed to take as many as 49 days to pupate, with mean

TABLE 4

Effect of crowding on larval development of S. chloropterus

Larvae per pan	Exps.	Total larvae	% pupae	Mean larval period (days)
100–200	8	1174	57.8	14.7
200–400	9	2761	60.0	13.9
400–800	8	4510	62.3	14.3
800–1000	1	963	60.5	17.5

larval periods of 25.7 and 29.5 days, when fed exclusively on Pablum or on Pablum and live larvae of *Haemagogus equinus* and *Anopheles albimanus*. This would seem to indicate that yeast is one of the foods of preference for rearing this species in the laboratory. The addition of living mosquito larvae to the diet does not seem to accelerate development.

Table 4 gives the results of experiments made to determine the effect of crowding on the rate of pupation and on the length of the larval period. In these experiments we used round, white-enamel pans measuring approximately 10 inches in diameter at the water level. It may be noted that there appears to be no difference between the percentages of larvae reaching the pupal stage in any of the pans regardless of the number of larvae, ranging from 100 to 1,000. When more than 800 larvae were reared in a single pan there seemed to be a marked increase in the mean duration of the larval period.

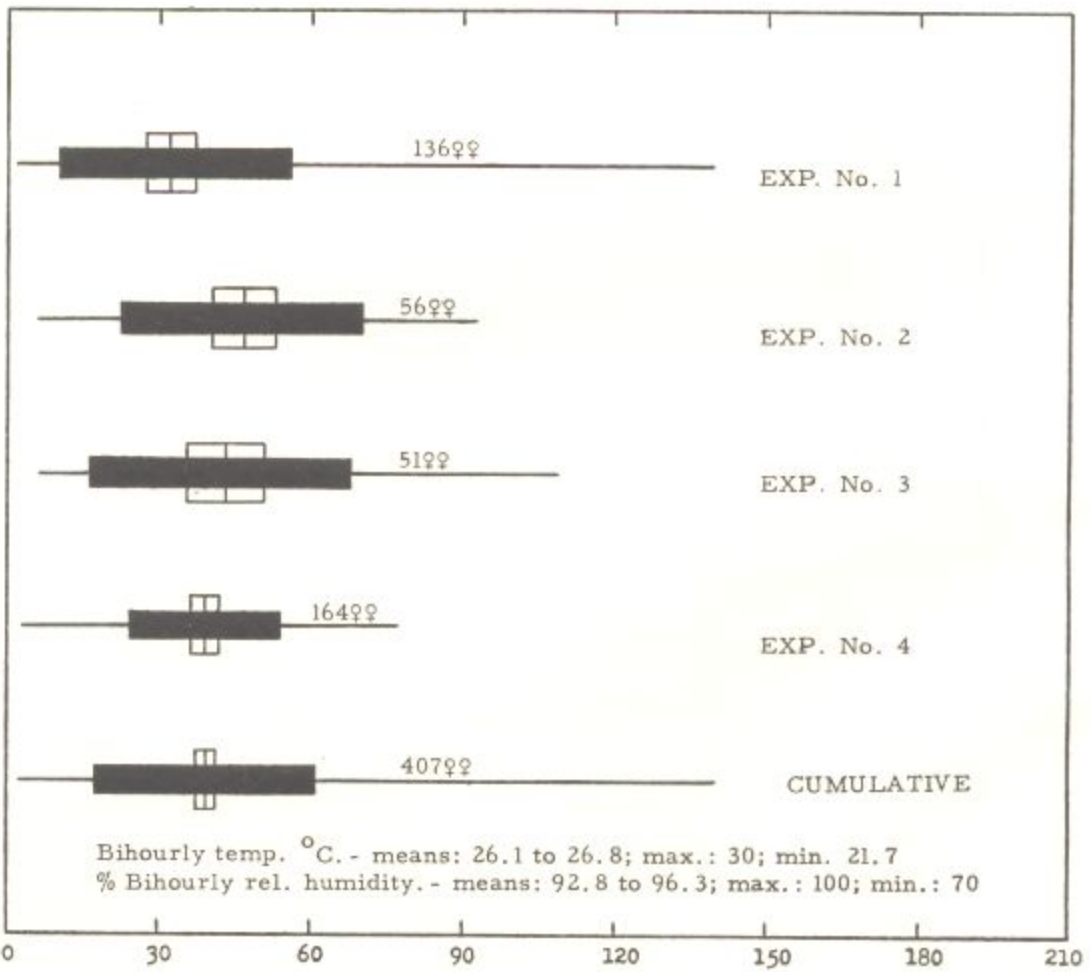

FIG. 5

THE PUPAL STAGE

As in most other sabethines, the pupa of *S. chloropterus* develops very slowly. In one experiment run at a mean bihourly temperature of 26°C, in which the number of hours from pupation to emergence was measured for 1,607 pupae, the average length of the pupal stage was 150 hours with a minimum of 123 hours (one specimen) and a maximum of 160 hours (482 specimens).

FEMALE LONGEVITY

Four experiments were made to determine the life span of *S. chloropterus* females under laboratory conditions in order to apply this knowledge to future transmission work with yellow fever virus. In these experiments, females were removed from a fresh stock colony immediately after engorging with blood for the first time, and transferred to colony cages. These mosquitoes were treated in the same manner as described earlier in this paper for the stock colony. If we consider that the life span in these experiments was measured from the time of the first blood meal until death, then it becomes obvious that the real longevity of these specimens is from 5 days to 4 weeks longer than shown, since it has already been pointed out above that *S. chloropterus* females do not begin to take blood until the fifth day after emergence and that it may be as long as 4 weeks before all the females of a particular brood take a blood meal.

In Figure 5 are plotted the results of the four experiments, as well as the cumulative data of all of them. The length of the thin center line in each of the columns represents the life span; the solid, broad, black stripe is one standard deviation from the mean; the hollow quadrangle represents twice the standard error and the cross bar is the mean duration of life in each case. As can be observed in this figure, while the maximum longevity showed much variation (from 78 days in Exp. No. 4 to 140 days in Exp. No. 1) the mean longevity (32.5 days in Exp. No. 1 to 46.8 days in Exp. No. 2) falls very nearly within the expected variation in random samples of a population, especially if it is considered that the four experiments were run under somewhat variable environmental conditions.

It is of interest to compare the cumulative mean longevity of the four experiments, which was 38.9 days with a maximum of 140 days, with that given by Jachowski (1954) for *Aedes polynesiensis* (the vector of filariasis in Samoa) which was 21.2 days with a maximum of 56 days.

TABLE 5

Survival rate of S. chloropterus *females after initial blood meal*

Weeks after 1st blood meal	Per cent survival				
	1st exp.	2nd exp.	3rd exp.	4th exp.	Cumulative data all exps.
1	96.3	98.2	96.1	98.2	97.3
2	88.2	87.5	78.4	89.0	87.2
3	71.3	78.6	66.7	81.7	75.9
4	45.6	75.0	62.7	72.6	62.7
5	25.0	60.7	62.7	65.2	50.9
6	20.6	58.9	54.9	45.7	40.3
7	20.5	53.6	51.0	26.8	28.0
8	10.3	42.9	45.1	11.0	18.9
9	8.8	32.1	39.2	1.2	12.5
10	8.1	12.5	29.4	0.6	8.1
11	7.4	8.9	19.6	0.6	5.4
12	4.4	5.4	7.8	0	3.2
13	2.9	1.8	5.9	—	2.0
14	2.9	0	2.0	—	1.2
15	2.9	—	2.0	—	1.2
16	2.9	—	0	—	1.0
17	2.5	—	—	—	1.0
18	2.2	—	—	—	0.7
19	2.2	—	—	—	0.7
20	0	—	—	—	0

Table 5 gives the survival rate of *S. chloropterus* females in the four experiments mentioned above, as well as the cumulative data of all four experiments together. From the last column we may observe that 50 per cent of the females lived between 5 and 6 weeks after the initial blood meal, and that a mortality of 90 per cent did not occur until after the ninth week. It would be of interest to repeat these experiments under constant temperatures and to compare the longevity of this species with that of other known vectors of sylvan yellow fever, such as *Haemagogus spegazzinii*, *H. equinus* and *H. lucifer*.

SUMMARY

A colony of *S. chloropterus* was established in 1-meter cubical cages. A trussed guinea pig or rhesus monkey served as the source of blood for the females, while a cotton ball soaked in sugar solution and hung from the top of the cage made available the necessary carbohydrates for both males and females. A well-ripened section of bamboo closed with a lid and with a 1-inch hole through its side was used as an oviposition re-

ceptacle. Larvae were reared in round enamel pans 10 inches in diameter in a yeast-infusion medium.

S. chloropterus was found to be strictly diurnal in habits. Females seek a blood meal in greatest numbers during the early afternoon hours (1400–1500). Both males and females become engorged on sugar solution from 6 to 24 hours after emergence. No female has been observed feeding on blood before the fifth day after emergence and the peak of biting activity is not reached until the second or third week. Females prefer to bite high on the body having a special predilection for the nose and lips.

S. chloropterus is a stenogamic species. Mating occurs while resting on a surface and is preceded by peculiar prenuptial activity on the part of the males. Copulation lasts from 4 seconds to 34 minutes, with an average time of 6 minutes. Mating has not been observed before the sixth day after emergence and the peak of mating activity is not reached before the second or third week of the female's life. Insemination does not necessarily occur before the first blood meal and does not appear to be essential for ovarian development.

Females oviposit by hovering in front of the hole in the bamboo section and forcibly ejecting one or two eggs through the hole and into the water in the bamboo. The position of the sun in the sky rather than light intensity seems to be the determining factor in inducing oviposition. The greatest percentage of eggs are laid in early afternoon (hours 1200–1500). The species was found to be nonautogenous, that is to say, it must have a blood meal before egg-laying takes place. Oviposition usually begins on the third day after a blood meal and goes on through the thirteenth day. The average number of eggs per female after a single blood meal is 38.6 with a minimum of 2 and a maximum of 103. Each female may lay an average of 138 eggs during her life time. Females exercise a definite preference for ovipositing in a bamboo with closed top and a 1-inch hole through the side rather than in a bamboo with open top.

The eggs of *S. chloropterus* are rhomboid in shape, the embryo develops in 3 to 4 days at room temperature and the eggs hatch soon after the larvae attain full development inside, being incapable of going into a prolonged diapause. The larvae are facultatively predaceous and cannibalistic but they do not frequently attack larvae of their own species, when in the same stage of development. They do not swallow the prey but suck the body contents through punctures in the cuticle.

The mean period spent by larvae from hatching to pupation at 26°C, is 14.8 days with a maximum of 28 days and a minimum of 9 days. The mean developmental period of pupae at this temperature is determined to be 150 hours with a maximum of 160 hours and a minimum of 123 hours.

The mean life span of females after the initial blood meal at mean temperatures of 26.1 to 26.8°C and a mean relative humidity of 92 to 97%, was found to be 38.9 days with a maximum of 140 days. It was also determined that 50 per cent of these females live between 5 and 6 weeks after taking their first blood meal and that 9 to 10 weeks elapsed before 90 per cent of these females died.

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