OBSERVATIONS ON THE DEVELOPMENT CYCLE OF AEDES (F.) TOGOI UNDER LABORATORY AND NATURAL CONDITIONS

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/ Following is the translation of an article by K. P. Chagin, Military Surgeon II Rank, N-unit Viral Laboratory (Head - V. A. Eskin, Military Surgeon II Rank), published in the Russian-language periodical Meditsinskaya Parazitologiya i Parazitarnyye Bolezni (Medical Parasitology and Parasitic Diseases), 12(2): 44--52, 1943. Translation performed by Sp/7 Charles T. Ostertag, Jr. /

Aedes (F.) togoi, along with Culex pipiens var. pallens, and Culex tritaeniorhynchus, are noted by Japanese authors (Mitamura, Jamada, and others) as one of the main carriers of Japanese encephalitis. The investigations of P. A. Petrishcheva and A. A. Smorodintsev, which were conducted in 1940, demonstrated its role in the transmission of this disease also in the Primorskoy Kray. Nevertheless, up until recently in the USSR the biology of Ae. (F.) togoi has not been the subject of a special study. This species was detected for the first time in Primorskoy Kray in 1927 by A. A. Shtakelberg; in 1940 P. A. Petrishcheva detected a mass breeding site for these insects on the rocky sea shore in Posyet and in Zarubin (Khasanskiy Rayon). For the data which has accumulated since then on the field ecology of this species see the article by Chagin and Kondratyeva which is in this same issue of the journal. In 1941--1942 we studied the duration of the development cycle of Ae. (F.) togoi under natural conditions and under various temperatures under laboratory conditions. We are exposing the results of these observations in the present article.

Methods of operation. Under laboratory conditions the tests were set up at constant temperatures and under conditions of various fluctuations in it. A constant temperature was maintained at a level of 15, 20, 25, and 30°. At 35--37° we observed the very high death of the larvae and therefore we did not conduct systematic observations at these temperatures. In the second series of tests the temperature fluctuations were established in the following limits: 15--18°, 18--21°, 20--25°, and 20--29°. The tests were set up in wooden insectaria with the dimensions of 80x80 cm. The side walls, corresponding to the conditions of the test, could be made of plywood or gauze. Regulation of the temperature was carried out with the help of electric bulbs of 40--100 candles and with the help of the side walls of the insectarium (replacing the plywood with gauze). The breeding place with fed mosquitoes was placed in a specific insectarium; a glass cuvette with water and stones projecting out over the water was set up in the breeding tank (creating conditions for egg laying).

For observing the individual layings a replete female was placed in a small flask into which a little water was poured and pebbles which protruded above the level of the water were deposited. The larvae were maintained in 10-liter glass jars, into which 2--3 liters of water was poured and rocks were placed. Optimal feeding conditions were created for the larvae; fresh green filamentous algae were added regularly.

Observations in nature were conducted at a point which was located on a rocky sea shore. Observations were made in natural reservoirs, and besides this small artificial reservoirs were created in small, previously dry, depressions in stony clumps and in small rock fissures. The site for setting up such reservoirs was selected no less than 0.5 km from the natural ones in order to avoid the laying of eggs in the test reservoirs by mosquitoes which are not included in the test (the range of active flight of this species is no more than 400--500 meters).

The captured mosquitoes were fed on horses, after which in the breeding tanks they were placed in a natural habitat. After egg laying, the stones on which the eggs were laid were placed in the established reservoirs and further observations were kept over these. Measuring the temperature of the water and the air was done three times a day, at 7, 13, and 19 hours. Under natural and laboratory conditions note was made of the date of blood sucking, egg laying, emergence of larvae, their molting, pupation, and attainment of wings.

Results of Laboratory Observations

For the laboratory tests of 11 May, larvae were collected which had emerged from eggs which had passed through the winter. Larvae II and III were predominant in the collections; there were very few larvae IV. From these larvae, adult mosquitoes developed which were placed in the 80x80 cm breeding tanks and maintained up to 10 days. The tank was humidified and the mosquitoes fed with a weak solution of sugar. During this time a large portion of the mosquitoes copulated. Both we, as well as, A. I. Lisova were able to observe the copulation of mosquitoes of this species in smaller sized breeding places (30x30 cm).

During the course of the stated period the females were fed on white mice, transplanted into breeding places for egg laying and maintained in insectaria at a specific temperature.

It is necessary to note the very high degree of "greediness for blood" on the part of females of this species of mosquitoes: A. I. Lisova and we were able to observe repeated blood sucking while digested blood from a previous blood sucking was still present. Repeated blood sucking is also observed following the final digestion of blood which was taken initially, but still prior to oviposition of eggs which already mature. This biological peculiarity of Ae. (F.) togoi has a specific epidemiological significance, since it may be a factor, causing the great feasibility for the transmission of the causative agents of various infections by them. One blood sucking, even if incomplete, turns out to be sufficient for the maturation and oviposition of a specific portion of eggs.

In our tests egg laying was noted in the following periods following blood sucking: At a temperature of 15° - after 9--11 days, at 20° - after 7--10 days, at 25° - after 6--8 days, and at 30° - after 5--7 days. These facts basically conform with the data of A. I. Lisova, who in 1940 observed egg laying in Ae. (F.) togoi at a temperature of 15° after 12 days, at 17° after 9 days, and at 21° after 6 days.

The average number of eggs in an egg mass is 106; extreme variants are 174 and 21. The sharp fluctuations in the number of eggs laid are found in direct dependency on the amount of blood taken by the female; following the intake of a full portion of blood we observed the maximum egg masses, and following the intake of an incomplete portion the egg mass was reduced in proportion to the reduction in the amount of blood taken in. Such a high degree of gonotrophic harmony is described by T. S. Detinova (1942) also for certain other species of Aedes.

Ae. (F.) togoi lay their eggs on the surface of the rocks which border the water level or on the wall of the jar. In laying the eggs, the female attaches them closely to roughnesses in the rocks or to the wall of the vessel, immersing them into the water only by ½--2/3. Under laboratory conditions the females also lay eggs on filter paper. Not once were we able to observe in this species egg laying on the surface of an aqueous film. The form of the egg is oblong-oval, somewhat pointed from one side. The length exceeds the width by 3½--4 times; the color is intensively black.

The emergence of the larvae from the eggs was noted after the following periods: At a temperature of 15° - after 10 days following oviposition, at 20° - after 8 days, at 25° - after 7 days, and at 30° - after 5 days. The emergence of larvae is not harmonious. Under laboratory conditions a lengthiness was observed in the periods of emergence of the larvae: At a temperature of 15° - up to 23 days, at 20° - up to 21 days, at 25° - up to 22 days, and at 30° - up to 27 days. During the course of the first 5-day period from the initial appearance of larvae, emergence was noted from 38% of the eggs, during the second 5-day period - from 31%, during the third - from 20%, during the fourth - from 9%, and during the fifth and sixth - from 2%. Thus, the larvae emerge from the main mass of eggs during the first 10 days (from the onset of emergence of the first larvae).

The duration of metamorphosis is presented in table 1 for constant temperatures. The difference in the duration of individual stages fluctuates within the limits of 1--2 days.

Mosquitoes which hatched from larvae maintained at a temperature of 15 and 20° were the largest, and those which emerged at 30° were the smallest and least capable of living. At 30° a larger percentage of death of larvae was noted than at the lower temperatures. In breeding tanks with a constant temperature of 25° mosquitoes of average sizes emerged, they were more active in comparison with other mosquitoes, and the percentage of death of larvae at this temperature was relatively low.

Thus, the optimum constant temperature for the development of Ae. (F.) togoi should be considered as 25°.

A constant temperature of 30° is already oppressing; at 35--37° an insignificant portion of the larvae survive.

In our tests, following the first egg laying the majority of the females died; no more than 8--10% of all the test females survived and were capable for repeated egg laying.

Part of the females were maintained on sugar syrup and, just as with A. I. Lisova, we were not able to observe the laying of eggs by these females, the ovaries developed only up to the II--III phase. Thus, in Ae. (F.) togoi, just as in the majority of mosquitoes, autogenic maturation of the ovaries is not observed; blood feeding is necessary for their development. In the presence of blood feeding it is subjected to the law of gonotrophic harmony.

Under natural conditions in reservoirs a constant temperature is never observed, therefore we introduced the factor of temperature fluctuation into the test. The duration of individual phases of development of Ae. (F.) togoi during various fluctuations of temperature are presented in table 2.

These observations show that the development of Ae. (F.) togoi under temperature fluctuations takes place somewhat more rapidly than at a constant temperature, and even more rapidly than at a constant temperature which equals the upper limit of fluctuation. If at a temperature of 25° development is concluded in 29--51½ days, then at a temperature of 20--25° it is concluded in 25--45 days. The same picture is observed when comparing the periods of development at other temperatures.

Above we noted the depressing action of a constant temperature of 30°, which is manifested in the emergence of smaller, less active, and weaker mosquitoes, and a high percentage of death of the larvae. The depressing effect of this temperature would not be observed if it were the upper limit of fluctuation. In the tests with temperature fluctuations the mosquitoes which emerged at 20--29° were of average size and very active. Consequently, under the conditions of a variable temperature the border of the temperature optimum for development is expanded.

During temperature fluctuations the development of Ae. (F.) togoi proceeds approximately 20% more rapidly than at the corresponding constant temperature.

For determining the lower temperature threshold of development we maintained the larvae at a temperature of 5--7° and 2--5°; in the first case single moltings of larvae were observed, and in the second case not one molting took place in the course of 3 months. These observations make it possible to consider the lower threshold of development for Ae. (F.) togoi as a temperature of 5°.

The observations which were carried out under natural conditions supported these conclusions. It is possible to find the first larvae starting with the beginning of April (3--5 Apr 1942) when the average temperature for the southern coastal regions of Primorye do not exceed 5--7°. The emergence of larvae from the eggs and their further development under natural conditions are concluded in the second half of October, when the average temperature drops to 7--9°, and the minimum to -0.6 to -1.6°. Late in fall it is possible to find the larvae of Ae. (F.) togoi under a film of ice (Kondratyev, 22 Nov 1941; Chagin, 26 Nov 1941).

Thus, under the natural conditions of the southern regions of Primorskoy Kray the development of Ae. (F.) togoi is possible from the first half of April up to the second half of October. The larvae and pupae which do not reach emergence by the end of October do not undergo further development and die with the onset of the cold and the freezing of the reservoirs.

The wintering stage of Ae. (F.) togoi is the egg stage. Observations, conducted under laboratory conditions on the larvae of late collections (26 Nov 1941), testify that in mosquitoes of this species there is a clearly expressed retardation in the development of larval stages of late generations. The following larvae were collected on 26 Nov: Stage I -- 6 specimens, II - 62 specimens, III - 111 specimens, and IV - 30 specimens. They were maintained under laboratory conditions at a temperature of 20--25°. Under these conditions we observed the exceedingly prolonged development of each stage. Thus, emergence began only on 18 Jan, that is, in almost 2 months following collection, and ended on 21 Mar. The development of each stage went 7--8 times slower than the development of larvae of the spring and early summer collections at this same temperature. This suggests an analogy with the data of Netskiy (1941) on the effect of low temperatures on the embryonic development of A. maculipennis.

The behavior of Ae. (F.) togoi larvae in a reservoir is very characteristic. They are frightened and with the least disturbance rapidly descend to the bottom and go under rocks or enter various fissures in them. On the bottom the larvae and the pupae may remain for quite a long time, being attached at various angles to the surface of the rocks. The larvae feed on detrital, which is found in the form of a sediment on the rocky bottom of the reservoir or on green filimentous algae which very often completely cover the entire bottom of the reservoir. During the time of feeding the larvae are as if "crawling" along the bottom or along the surface of the rocks, or are held at an angle ("position of a scraper") and, moving slowly, without tearing the mouth organs away from the surface of the rock, scrape the deposit from it. In a resting state the larva may be observed as if lying on the surface of the bottom rocks.

In the course of a season we considered the field composition of generations. Both in the laboratory as well as under natural conditions we were able to carry on these observations for three generations. In the 1st generation, males made up 66%; during the course of the season a relative decrease took place in the number of males and an increase in the number of females. Beginning with the 3rd generation a sharp predominance of females over males is noted; in the 2nd generation the males made up 53.9%, and in the 3rd -- 21.3%.

This biological peculiarity is also important from an epidemiological point of view: With the general increase in the number of mosquitoes during the course of the season, a significantly greater increase takes place in the number of females, which determines their greater concentration in foci by the beginning of the epidemic period. The relationship between males and females in generations which were hatched both under laboratory as well as natural conditions is almost the same and differs only in terms of percentages (fig. 1).

Results of observations under natural conditions

Systematic observations of the length of the development cycle in Ae. (F.) togoi under natural conditions were conducted from 3 Jun through 20 Aug. The temperature of the water under natural conditions during this period was within the limits of 16 to 29°, with a daily fluctuation of from 2 to 8°.

The results of the observations under natural conditions are presented in table 3.

Based on temperature conditions, these mainly conformed to the laboratory test with a variable temperature of 20--29°. The period of development of individual stages in both cases was quite similar (compare tables 2 and 3). Under laboratory conditions at a temperature of 20--29° egg laying set in in 5--6 days following blood sucking, and under natural conditions - on the 5--7th day; the egg stage under laboratory conditions lasted 4½--22 days, under natural conditions - 8--33 days; the duration of development of all the larval stages under laboratory conditions was equal to 14--20 days, under natural - 14--19. The pupal stage under laboratory conditions was 4½--5 days, under natural - 5--7. The whole cycle of development under laboratory conditions at a certain variable temperature took place in 23--47 days, and under natural conditions - 27--59 days. Under natural conditions we noted a more prolonged development of the egg and pupa stages, due to which there is a certain lengthening of the entire cycle in comparison with the duration of it at the corresponding variable temperature under test conditions. In other respects almost complete conformity is noted in the data of the laboratory tests and the observations under natural conditions.

Thus, in an analysis of the results of the laboratory observations, conclusions can be made which are fully applicable to the corresponding natural conditions.

Number of possible generations for a season

It was pointed out above that under the natural conditions of the coastal southern regions of Primorskoy Kray the development of Ae. (F.) togoi is possible from the first half of April through the second half of October inclusively, that is, for a period of 6 months.

Knowing the average temperatures for these months and the limits of their daily fluctuations, and also the duration of individual phases under the corresponding temperatures, it is possible to calculate the number of possible generations in the course of a season in a given region. It is necessary to note the extreme lengthiness in the development of individual generations of Ae. (F.) togoi, which is mainly the result of the non-simultaneous emergence of larvae from eggs of the same laying. This biological peculiarity also conditions a conformity in the time of onset of development of the subsequent generation with the period of greatest development of the generation preceeding it, due to which no pure generations are observed in the certain species. In each individual reservoir during the entire season the age composition of the larval population is always exceedingly irregular. We will turn our attention to an analysis of the calendar of individual generations (figure 2).

The emergence of larvae of the 1st generation (from overwintering eggs) begins with the first days of April and ends in the middle of May. The emergence of mosquitoes of this generation may be observed from the end of the first to the beginning of the second half of May up until the twenties of June. Thus, from the beginning of the development of the eggs up until the onset of emergence of the 1st generation approximately 45--46 days pass, and up until the end of emergence - 80--83 days. The laying of eggs by the females of the 1st generation is observed from 23--28 May up to 25--30 June, consequently the egg stage of the 2nd generation is encountered from the last days of May up until the twenties of July. The emergence of mosquitoes of the 2nd generation begins with the last days of June and ends in the middle of August. From the onset of maturation of eggs in mosquitoes of the 1st generation up until the onset of emergence of mosquitoes of the 2nd generation, 37--40 days pass, and up until the end of emergence - 88--90 days. Egg laying by mosquitoes of the 2nd generation is noted from 29--30 June up until 25--30 August, consequently the egg stage of the 3rd generation is encountered in nature from the first days of July up to the middle of September (the development of the last egg mass of the 2nd generation is concluded). The onset of emergence of mosquitoes of the 3rd generation is noted in the end of July and is concluded in the middle of October. From the onset of maturation of eggs in the females of the 2nd generation until the onset of the emergence of mosquitoes of the 3rd generation, an average of 28--30 days pass, and until the end of emergence - 105--107 days. The egg stage of the 4th generation begins with the first days of August. The emergence of larvae takes place only from the earliest egg masses, made by mosquitoes of the 3rd generation. Those egg masses, the development of which is not concluded by the onset of an average temperature equal to the low threshold (4--5^{o}), remain for hibernation. The onset of emergence of this generation is possible from the last days of August to the first days of September. From the onset of maturation of eggs in the mosquitoes of the 3rd generation to the onset of the emergence of mosquitoes of the 4th generation, an average of 30 days passes. The emerging mosquitoes of the 4th generation lay eggs from the end of the first half of September, but up until the onset of the low threshold temperature only larvae from the first eggs may emerge, and they develop only up to stage II and III. With the onset of cold and the freezing up of the reservoirs they die. The main mass of eggs laid by females of the 4th generation overwinter to the next season.

Thus, under favorable conditions Ae. (F.) togoi in the southern coastal regions of Primorskoy Kray (with the presence of suitable reservoirs for the entire season) may yield the emergence of mosquitoes of three complete generations and the incomplete emergence of the 4th generation. Mainly the masses of eggs laid by mosquitoes of the 4th and 3rd generations remain over winter.

During unfavorable conditions -- a strong drying up of reservoirs or a complete drying up for a certain period, when the eggs are above the level of the water -- the development of larvae from the egg masses of any generation is held back, and may take place only with the repeated filling of the reservoirs with water. In the course of a season a shortening of the minimum duration of development takes place and an increase in the maximum (from the beginning of the egg stage until the end of emergence). The shortening of the minimum periods takes place as a result of an increase in the average temperature and a shortening, as a result of this, of the duration of development of each stage. A parallel increase of the maximum periods takes place in view of the stretching out of the egg stage and the non-similarity in the emergence of winged mosquitoes. The influence of these factors on lengthening the maximum period is expressed to a greater degree with each generation.

The observations which were carried out for the course of two seasons under natural conditions, and also the data from experiments have established the following main dates for the period of active life of Ae. (F.) togoi under the meteorological conditions of southern Primorye (table 4).

The epidemic period of fall encephalytis in the Primorskoy Kray is registered from the beginning of the second half of August through the first half of October inclusively. Consequently, the greatest epidemiological importance belongs to mosquitoes of generations III and IV; the first early cases of the disease may be caused by the bites of infected mosquitoes of generation II.

Practical Conclusions

In organizing the struggle with Ae. (F.) togoi there is great importance in the sharply expressed focalness of distribution of this species and the quite limited range of active flight.

The range of flight from typical sites of residence and breeding deep in the heart of the mainland or an island, and similarly along a nonrocky shore, is not great - no greater than 300--500 meters. This circumstance is a very important factor in selecting a new site for a permanent or temporary placement of human collectives in coastal regions. In these cases we should select sectors which are situated at a distance no closer than 1 km from habitats of the sea shore which are typical for the residence of Ae. (F.) togoi. By observing this condition, new populated points will not be subjected to the mass migration into them of mosquitoes of this species.

Exclusive places for the breeding of Ae. (F.) togoi are the small, rocky reservoirs on the rocky sea coast. The sites for laying eggs are strictly specific: The surface of rocks even with the level of the water. The area of the reservoirs is small, it does not exceed several square meters. The larvae are nourished by bottom feeding on green filamentous algae and substances which settle on the surface of the submerged rocks. All these peculiarities make it possible to take into consideration the reservoirs which serve as breeding places for these mosquitoes and to opportunely treat them with larvicides.

Our experiment in treating these reservoirs by the usual methods (oil treatment, suspension of Paris green) demonstrated the high degree of effectiveness of these methods. For the treatment of togoi reservoirs we recommend the use of an aqueous suspension of Paris green, which will cause the complete death of the larvae.

The possibility of the complete exposure and registration of togoi reservoirs, their small area, the specific sites for laying eggs -- all of these are conducive to carrying out radical measures and create the possibility of the very rapid liquidation of foci of mass breeding of Ae. (F.) togoi.

It seems possible to us to use specific methods for treating togoi reservoirs; in particular it is necessary to test the method of greasing the surface of the rocks which border on the water level with oily-adhesive substances which prevent the development of eggs which have been laid and do not permit subsequent egg laying.

As was pointed out above, the development of this species of mosquitoe in the southern regions of the Primorskoy Kray is possible from the first half of April through the first half of October inclusively, and this determines the period for carrying out antilarval measures.

Conclusions

1. Ae. (F.) togoi in the southern regions of Primorskoy Kray may yield the emergence of four generations, the last of which is incomplete. Out of some of the eggs laid by females of generation IV larvae develop, but their development does not reach the stage of emergence, and with the freezing of the reservoirs they die. Mosquitoes of generations III and IV have the greatest epidemiological importance.

2. Under constant temperatures, the development of the water stages of

Ae. (F.) togoi is possible to some degree within the limits of from 5 to 35--37°. The optimum temperature for development is found within the limits of 24--27°.

3. With fluctuations in temperature the development is speeded up by 20% and the limit of the temperature optimum is expanded in the direction of a higher temperature; fluctuations reach an upper limit of 30--32°.

4. Under all conditions of observation a characteristic peculiarity is noted for Ae. (F.) togoi -- a great scattering in the periods of emergence of larvae from eggs of the same laying. This explains the lengthiness of the generations.

5. In the first two generations a predominance of males is noted, but with generation III the females clearly predominate.

6. The wintering of Ae. (F.) togoi in Primorskoy Kray takes place in the egg stage. Wintering is carried out mainly by the egg masses of mosquitoes from generations III and IV.

7. The sharply expressed focalness in the distribution of this species and the specific, strictly favored, larval biotopes create the possibility for the liquidation of foci of mass breeding of Ae. (F.) togoi in the course of a short period of time.

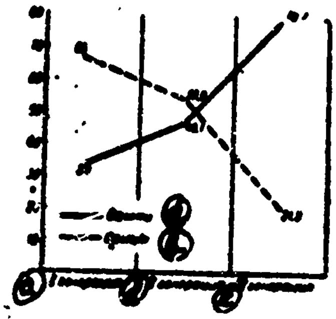

Figure 1. Ratio of males and females in generations of <u>Aedes (F.) togoi</u> (in percentages).

a - Females; b - Males; c - Generation I; d - Generation II; e - Generation III.

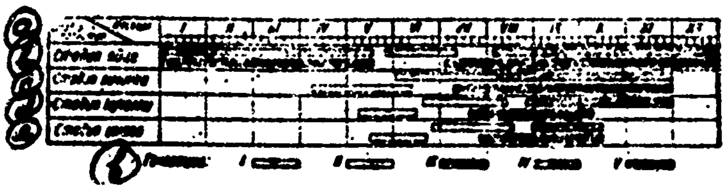

Figure 2. Calendar of generations of <u>Aedes (F.) togoi</u>.

a - Stage of development \ Month
b - Egg
c - Larva
d - Pupa
e - Imago
f - Generation

Table 1

Period of development of *Ae. (F.) togoi* under constant temperatures (in days)

Water temperature	Period of maturation of eggs in the mosquitoe	Length of aqueous stages							% death of larvae
		Egg stage (0)	L I	L II	L III	L IV	Pupal stage (P)	All told	
15°	9--11	10-23	6-8	6-8	5-7	6-8.5	5-6.5	38-60.5	34.5
20°	7--10	8-21	6-7	6-8	4-6.5	5-7	5-6	34-55.5	37.5
25°	6--8	7-22	5-6	4-6	4-6	5-6	4-5.5	29-51.5	34.0
30°	5--7	5-27	4-6	4-5	4-5.5	3-4.5	4-5	24-52	75.5
35-37°	Due to the large percentage of death, observations of mass numbers could not be carried out								

Table 2

Period of development of *Ae. (F.) togoi* under variable temperatures (in days)

Water temperature	Period of maturation of eggs in the mosquitoe	Length of development						
		Egg stage (0)	L I	L II	L III	L IV	Pupal stage (P)	All told
15--18°	7--11	7--14.5	5.5-8	6-7.5	4-5.5	5-8.5	5-8	32.5-52
18--21°	7--10	5.5--18	5.5-7	4.5-6	4-5	4-6	5-6.5	28.5-48.5
20--25°	6--7	5--17	5-6	4-5	3.5-6	3.5-5	4-6	25-45
20--29°	5--6	4.5--22	4-5	4-4.5	3-5.5	3-5	4.5-5	23-47

Table 3

Period of development of Ae. (F.) togoi under natural conditions (in days)

Water temperature	Period of maturation of eggs in the mosquito	Length of aqueous stages						
		Egg stage (0)	L I	L II	L III	L IV	Pupal stage (P)	All told
16--29° (daily fluctuation 2--8°)	5--7	8--33	3-4	4-5	3-4	4-6	5-7	27--59

Table 4

Data on the phenology of Ae. (F.) togoi in Primorye in 1941 and 1942

Generation	Onset of egg laying by females of the preceding generation	Appearance of larvae	Appearance of pupae	Emergence		Notes
				Onset	End	
First	Developed from over-wintering eggs	3-5 Apr	8-10 May	15-17 May	17-20 Jun	Some of the eggs remained for wintering
Second	23-28 May	2-3 Jun	18-20 Jun	23-25 Jun	12-13 Aug	
Third	29-30 Jun	5-7 Jul	16-17 Jul	20-25 Jul	15-18 Oct	
Fourth	1-3 Aug	6-9 Aug	25-28 Aug	4-2.IX(?)	Emergence not terminated	Large part of eggs remain for wintering
Fifth	7-10 Sep	15-17 Sep	Do not develop before emergence	Emergence of this generation not observed at all		