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LIFE HISTORIES ON VIRUS-INFECTED AND ON HEALTHY PLANTS

Henry H. P. Severin and Edward C. Klostermeyer

UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

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Genital characters, which are described and illustrated, indicate that the species occurring in California is identical with that occurring in Mexico. Color and markings are described in detail.

II. Transmission of California Aster-Yellows Virus . . . 544

Texananus incurvatus is the seventh phlepsid leafhopper that has been demonstrated to carry this virus. In single-insect tests, its efficiency in transmitting the virus was 22 per cent with celery, 1 per cent with asters. The virus was retained by single adults from 11 to 14 days.

III. Life History on Virus-infected and on Healthy Plants . . 546

The length of nymphal stages of *Texananus incurvatus* reared on healthy and on virus-infected plants did not differ significantly. On healthy plants, nymph mortality was high; on infected ones, negligible.

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Life Histories on Virus-infected and on Healthy Plants . . 553

Comparative life-history studies of these two species (selected for study because they experience no nymph mortality on either healthy or diseased celery plants) show no significant differences in the duration of nymphal stages between specimens reared on healthy celery and those reared on diseased celery. In *Colladonus montanus* the total duration of nymphal stages is shorter for the males than for the females. In both species, males were smaller than females. *C. geminatus* and *C. montanus* do not interbreed.

COLLADONUS GEMINATUS AND C. MONTANUS

LIFE HISTORIES ON VIRUS-INFECTED AND ON HEALTHY PLANTS¹

HENRY H. P. SEVERIN and EDWARD C. KLOSTERMEYER²

A recent paper (Severin, 1946) presented evidence that nine species of leafhopper vectors completed the nymphal stages on celery or asters infected with the California aster-yellows virus. The adults died, however, when transferred to healthy celery or asters. In life-history studies, the average total duration of the nymphal stages of *Texananus lathropi* (Baker) and *T. spatulatus* (Van Duzee) was less on infected than on healthy celery. Although *T. spatulatus* is not a vector of curly top, it required less time to complete its nymphal stages on curly-top sugar beets than on healthy ones; the difference, however, was not statistically significant.

This paper compares the intervals or periods between molts and the total duration of the nymphal stages of the geminate leafhopper, *Colladonus geminatus* (Van Duzee), and the mountain leafhopper, *C. montanus* (Van Duzee), reared singly on healthy celery plants and on celery plants infected with California aster yellows. These two leafhopper species were selected because no nymph mortality occurred on either healthy or infected celery plants. Other aspects of the life-history studies include mating, preoviposition period, oviposition, egg periods, and egg-laying capacity. Measurements of various parts of the body were taken of each nymphal instar and of the adults.

METHODS AND EQUIPMENT

Life-history studies of the two leafhopper species were undertaken with nymphs hatched from eggs deposited in the petioles of infected and of healthy celery plants. A day or two before the hatching period, the petioles in which oviposition occurred were cut in pieces and placed in stender dishes, the bottoms of which were covered with moist filter paper. Each nymph that hatched was transferred by means of a pipette to a diseased or healthy celery seedling, each enclosed in a cage. Daily examinations were made to determine each molt. Whenever a nymph molted, the exuvia was removed from the plant. The pipette and cages used have been illustrated in a previous publication (Severin, 1930).

LIFE HISTORY OF GEMINATE LEAFHOPPER, *COLLADONUS GEMINATUS*

Mating. Two of 10 pairs of the adult leafhoppers were in coition 5 and 6 days, respectively, after they acquired the winged stage.

¹ Received for publication July 6, 1948.

² Formerly graduate student in the Division of Entomology and Parasitology.

Preoviposition Period. During February, under greenhouse conditions, an attempt was made to determine the number of days required before egg deposition began. A male and a female after the last molt were kept in each cage enclosing a celery plant; daily examinations were made to determine when egg-laying began. The preoviposition period required from 7 to 13 days after the females acquired the winged stage. The females of 2 pairs observed in coition each began to deposit eggs 12 days after the last molt, and 6 and 7 days, respectively, after mating.

TABLE 3
DURATION OF EGG PERIODS AND DAILY EMERGENCE
OF NYMPHS OF TWO SPECIES OF LEAFHOPPERS
FROM HEALTHY AND INFECTED
CELERY PLANTS

Days from oviposition to hatching	Eggs on healthy celery		Eggs on infected celery	
	Nymphs hatched	Percentage of total hatched	Nymphs hatched	Percentage of total hatched
Geminate leafhopper, <i>Colladonus geminatus</i> ; eggs deposited October 29-30				
14.....	1	1.1	20	6.6
15.....	4	4.3	33	11.0
16.....	27	29.0	86	28.6
17.....	27	29.0	82	27.3
18.....	26	27.9	55	18.3
19.....	5	5.3	14	4.6
20.....	3	3.2	8	2.6
21.....	0	0.0	2	0.6
Total.....	93	300
Mountain leafhopper, <i>Colladonus montanus</i> ; eggs deposited August 16-17				
13.....	0	0.0	2	5.2
14.....	25	31.6	15	40.5
15.....	32	41.0	4	10.8
16.....	20	25.3	0	0.0
17.....	2	2.5	13	35.1
18.....	0	0.0	2	5.2
19.....	0	0.0	1	2.7
Total.....	79	37

Oviposition. In the process of oviposition, the female makes incisions in the margin of the celery leaves with her ovipositor, sometimes below the epidermis of the blade, and also in the veins and petioles, where she embeds a single egg in each slitlike egg chamber. Although occasionally laid singly, the eggs usually are deposited several in a row in the margin of the celery leaves or in the petioles. On rare occasions some females—probably near the end of natural life—deposit eggs on the surface of the leaves.

Egg. Measurements of 5 eggs indicate that the length of the egg ranges from 0.98 to 1.05 mm, with an average of 1.02 mm; the width from 0.22 to 0.25 mm, with an average of 0.24 mm. The egg is translucent when first

deposited but during the embryonic development turns white. It is elongated, narrower at one end than at the other, the distinction between dorsal and ventral surfaces being indicated by a difference in curvature. Near the hatching period, the pink eyes of the embryo become visible.

Egg Periods. The egg periods were determined from eggs deposited during October. Females were confined in cages enclosing healthy and infected celery plants and were transferred daily to successive plants for a period of 2 to 3 days. The plants in which eggs were deposited were covered with cages and examined daily for the hatching of nymphs. Eggs deposited during 1 day hatched over a period of 8 days. A daily count of the nymphs hatched in each cage was taken. The egg periods, with the number and percentage of nymphs that hatched, are shown in table 3.

There were no marked differences in the percentages of the total nymphs hatched daily from eggs deposited in healthy and infected celery. The egg periods varied from 14 to 21 days with eggs deposited during October.

Hatching. The nymph, enclosed in the chorion and egg membranes, pushes out of the slitlike aperture of the egg chamber during the process of hatching. After its extrication from the eggshell and embryonic membranes, it remains suspended with the tip of the abdomen in the embryonic envelopes and with legs sprawled apart. When the exoskeleton hardens, the nymph crawls away and usually settles on the lower surface of the leaf to take its first meal.

Molting. Certain indications appear a day or two before the nymph molts. The body becomes distended, the membranous connections between the head and thorax, thorax and abdomen, and between the abdominal segments become greatly stretched, and the abdomen shows a rounding out. During the process of molting, the nymph inserts the setae into the tissue of the plant and firmly clasps the petiole or leaf with the claws. After molting, the nymph remains suspended with the tip of the abdomen in the exuvia and with legs sprawled apart. The adult is white in color after the last molt, and the wings expand rapidly. The elytra are held away from the lower wings until the exoskeleton hardens.

Color of Nymphal Instars and Adults. Recently hatched nymphs are white with pink compound eyes. Within a few hours after the molt, the bodies develop a faint color pattern, which becomes more pronounced a few days later. There are two nymphal color patterns (plate 2): one in which each instar is mottled with yellow and brown, and one in which each instar is marked with black bands on the thorax and some of the segments of the abdomen. There is no marked difference in the color patterns of male and female adults reared from mottled nymphs and of those reared from black-banded nymphs (plate 2).

Duration of Periods Between Molts. A comparison was made of the intervals or periods between molts and the total duration of the nymphal stages and egg periods of mottled and black-banded nymphs, reared singly on healthy and diseased celery plants (table 4). The males reared from mottled nymphs required 26.6 days to complete the nymphal stages on healthy celery and 24.0 days on infected celery; the females required 28.5 days on healthy celery and 29.6 days on infected celery. Of those reared from black-banded nymphs, one male required 27 days on healthy celery and two males an aver-

TABLE 4
DURATION OF EGG AND NYMPHAL STAGES OF TWO SPECIES OF
LEAFHOPPERS ON HEALTHY AND ON INFECTED
CELERY PLANTS

Date hatched	Duration of egg and nymphal stages, days							Total nymphal stages, days	Total egg period and nymphal stages, days
	Egg period	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar		
Males of geminate leafhopper, <i>Colladonus geminatus</i> , reared from mottled nymphs on healthy celery plants									
November 15.....	17	6	3	4	4	7	..	24	41
November 15.....	17	6	5	3	5	7	..	26	43
November 15.....	17	9	3	4	4	7	..	27	44
November 15.....	17	6	5	6	3	8	..	28	45
November 16.....	18	8	4	4	3	4	..	25	43
November 16.....	18	8	4	4	3	7	..	26	44
November 16.....	18	7	4	5	3	9	..	28	46
November 16.....	18	8	4	4	4	10	..	30	48
November 17.....	19	6	4	5	3	8	..	26	45
Average.....	17.6	7.1	4.0	4.3	3.5	7.4	..	26.6	44.3
Males of geminate leafhopper, <i>Colladonus geminatus</i> , reared from mottled nymphs on infected celery plants									
November 14.....	17	7	3	4	4	6	..	23	41
November 14.....	17	7	3	4	4	6	..	23	41
November 15.....	18	5	3	4	4	6	..	22	40
November 15.....	18	9	3	4	4	7	..	27	45
November 16.....	19	6	4	5	3	7	..	25	44
Average.....	17.8	6.8	3.2	4.2	3.8	6.4	..	24.0	42.2
Females of geminate leafhopper, <i>Colladonus geminatus</i> , reared from mottled nymphs on healthy celery plants									
November 15.....	17	7	3	4	5	7	..	26	43
November 15.....	17	8	4	3	6	6	..	29	46
November 15.....	17	8	5	6	3	8	..	30	47
November 16.....	18	6	5	4	4	9	..	28	46
November 16.....	18	7	5	4	4	8	..	28	46
November 17.....	19	5	5	4	4	9	..	27	46
November 17.....	19	7	4	4	3	14	..	32	51
Average.....	17.8	6.8	4.4	4.1	4.1	8.7	..	28.5	46.4
Females of geminate leafhopper, <i>Colladonus geminatus</i> , reared from mottled nymphs on infected celery plants									
October 23.....	15	8	4	5	5	7	..	29	44
October 23.....	15	10	5	4	5	7	..	31	46
October 23.....	15	7	8	4	5	9	..	33	48
October 23.....	16	8	5	5	4	7	..	28	44
October 25.....	17	7	5	5	6	6	..	29	46
November 14.....	17	7	5	3	5	8	..	28	45
Average.....	15.8	7.8	5.3	4.3	5.0	7.3	..	29.6	45.5
Male of geminate leafhopper, <i>Colladonus geminatus</i> , reared from black-banded nymphs on healthy celery plant									
November 17.....	19	6	4	4	5	8	..	27	46.0

TABLE 4—Continued

Date hatched	Duration of egg and nymphal stages, days							Total nymphal stages, days	Total egg period and nymphal stages, days
	Egg period	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar		
Males of geminate leafhopper, <i>Colladonus geminatus</i> , reared from black-banded nymphs on infected celery plants									
November 15.....	17	8	3	4	4	8	..	27	44
November 16.....	18	4	4	3	5	7	..	25	43
Average.....	17.5	6.0	3.5	3.5	4.5	7.5	..	26.0	43.5
Females of geminate leafhopper, <i>Colladonus geminatus</i> , reared from black-banded nymphs on healthy celery plants									
November 15.....	17	7	5	4	4	10	..	30	47
November 16.....	18	6	4	4	4	8	..	26	44
November 17.....	19	6	2	2	5	4	8	27	46
November 17.....	19	6	4	2	3	4	9	28	47
Average.....	18.2	6.2	3.7	3.0	4.0	6.5	8.5	25.2	46.0
Females of geminate leafhopper, <i>Colladonus geminatus</i> , reared from black-banded nymphs on infected celery plants									
October 23.....	15	8	4	4	5	8	..	29	44
October 25.....	17	7	5	6	4	8	..	30	47
November 15.....	17	6	3	4	4	7	..	24	41
November 16.....	18	6	4	4	4	8	..	26	44
Average.....	16.7	6.7	4.0	4.5	4.2	7.7	..	27.2	44.0
Males of mountain leafhopper, <i>Colladonus montanus</i> , reared from nymphs on healthy celery plants									
August 16.....	14	4	4	4	5	7	..	24	38
August 16.....	14	5	4	4	3	2	6	24	38
August 16.....	14	5	4	5	5	6	..	25	39
August 16.....	15	5	5	4	5	6	..	25	40
August 16.....	14	5	4	3	2	5	7	26	40
August 16.....	14	5	5	3	5	11	..	29	43
August 16.....	14	9	5	5	5	7	..	31	45
Average.....	14.1	5.4	4.4	4.0	4.3	6.3	6.5	26.3	40.4
Males of mountain leafhopper, <i>Colladonus montanus</i> , reared from nymphs on infected celery plants									
August 16.....	17	5	3	5	5	7	..	25	42
August 16.....	13	6	4	5	5	7	..	27	40
August 16.....	14	7	4	5	4	7	..	27	41
August 16.....	15	5	5	5	5	7	..	27	42
August 16.....	15	6	5	7	4	7	..	29	44
Average.....	14.8	5.8	4.2	5.4	4.7	7.0	..	27.0	41.8

Table concluded on next page.

TABLE 4—*Concluded*

Date hatched	Duration of egg and nymphal stages, days							Total nymphal stages, days	Total egg period and nymphal stages, days
	Egg period	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar		
Females of mountain leafhopper, <i>Colladonus montanus</i> , reared from nymphs on healthy celery plants									
August 16.....	14	5	4	2	4	5	7	27	41
August 16.....	15	5	5	5	2	2	8	27	42
August 16.....	14	5	5	6	5	8	..	29	43
<i>Average</i>	14.3	5.0	4.6	4.3	3.6	5.0	7.5	27.6	42.0
Females of mountain leafhopper, <i>Colladonus montanus</i> , reared from nymphs on infected celery plants									
August 16.....	17	6	4	4	5	8	..	26	43
August 16.....	14	6	4	6	5	8	..	29	43
August 16.....	14	7	5	6	5	7	..	30	44
August 16.....	17	5	6	6	8	9	..	34	51
<i>Average</i>	15.5	6.0	4.7	5.5	5.7	8.0	..	29.7	45.2

age of 26 days on infected celery; the females required 25.2 days on healthy celery and 27.2 days on infected celery. The data show no significant differences in the length of the total nymphal stages between those reared on healthy celery and those reared on diseased celery.

Two females reared on healthy celery passed through 6 molts; all other males and females molted 5 times.

Measurements of Nymphal Instars and Adults. Table 5 gives the average measurements of various parts of the body 1 day after hatching and 1 day after each molt for 5 nymphs, 5 males, and 5 females of *Colladonus geminatus*. Each instar can be determined from the range of measurements: the diameter of the head across the compound eyes, and the length of the head, thorax, and abdomen. Average measurements of the male and female leafhoppers show that the males are smaller than the females.

LIFE HISTORY OF MOUNTAIN LEAFHOPPER, *COLLADONUS MONTANUS*

Measurements of Nymphal Instars and Adults. The average measurements of various parts of the body 1 day after hatching and 1 day after each molt of 5 nymphs, 5 males, and 5 females are given in table 5. Each instar can be determined from the range of measurements: the diameter across the compound eyes, and the length of the head, thorax, and abdomen. The males are smaller than the females.

Mating. Three of 10 pairs of adults copulated 5 days after the leafhoppers acquired the winged stage.

Preoviposition Period. Daily observations were made to determine the number of days required by females before egg-laying begins. The preoviposition period of 10 females required from 12 to 20 days, with an average of

13.9 days. Three females, observed mating, began to deposit eggs 5, 13, and 18 days later, and 11, 15, and 18 days, respectively, after the last molt.

Oviposition. The process of oviposition is similar to that described for *Colladonus geminatus*.

Egg. Measurements of 5 eggs indicate that the length of the egg ranges from 0.98 to 1.10 mm, with an average of 1.05 mm; the width from 0.25 to 0.32 mm, with an average of 0.29 mm.

TABLE 5
AVERAGE MEASUREMENTS OF INSTARS AND ADULTS OF TWO SPECIES OF LEAFHOPPERS

Nymphs and adults	Diameter of head across compound eyes, mm			Length of head, thorax, and abdomen, mm			Length of head to end of wings, mm		
	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean
<i>Geminate leafhopper, Colladonus geminatus</i>									
First instar.....	0.37	0.35	0.36	1.08	0.98	1.03
Second instar.....	0.49	0.45	0.47	1.54	1.45	1.48
Third instar.....	0.64	0.59	0.61	2.22	1.84	2.03
Fourth instar.....	0.86	0.79	0.82	2.57	2.45	2.51
Fifth instar.....	1.05	0.98	1.01	3.48	3.19	3.33
Males.....	1.16	1.08	1.12	3.92	3.68	3.80	4.80	4.32	4.56
Females.....	1.32	1.24	1.28	4.32	4.08	4.20	5.08	4.92	5.00
<i>Mountain leafhopper, Colladonus montanus</i>									
First instar.....	0.35	0.33	0.34	1.05	1.01	1.03
Second instar.....	0.49	0.47	0.48	1.62	1.49	1.55
Third instar.....	0.64	0.61	0.62	2.08	2.01	2.04
Fourth instar.....	0.79	0.74	0.76	2.45	2.37	2.41
Fifth instar.....	1.04	1.00	1.02	3.60	3.24	3.42
Males.....	1.12	1.08	1.10	3.92	3.64	3.78	4.20	4.04	4.12
Females.....	1.40	1.28	1.34	4.48	4.12	4.30	5.20	4.60	4.90

Egg-Laying Capacity. To determine how many eggs a single female deposits during her adult life, 1 female and 1 male after the last molt were confined in each cage enclosing a large healthy celery plant. The eggs were allowed to hatch; the total number of nymphs removed from each cage would equal the egg-laying capacity, provided that all of the eggs hatched. Since the nymphs and adults cause a rapid yellowing of the leaves, as reported in a previous paper (Severin, 1947), the female and male were transferred to a healthy plant whenever the celery became unfavorable as food. The nymphs were removed twice a month from each cage. The numbers that hatched from eggs deposited by each of 3 females were 289, 324, and 348, or an average of 320.

Egg Periods. The egg periods were determined from eggs deposited during August. Eggs deposited during 1 day hatched over a period of 7 days. The nymphs were removed daily from each cage and counted. The egg periods

with the number and percentages of nymphs that hatched are shown in table 3. The egg periods varied from 13 to 19 days.

Color of Nymphal Instars and Adults. The recently hatched nymph is white with pink compound eyes. Within a few hours after hatching, the body is yellow with black areas on the thorax and abdomen (plate 1). The color pattern of the second instar (plate 1) is similar to that of the first. The head, thorax, and abdomen of the third, fourth, and fifth instars are mottled yellow and pale brown (plate 1). The male and female of the summer generation are reddish brown, while the adults of the autumn generation are usually black (plate 1). The face is white or yellowish; a transverse reddish-brown band occurs between the compound eyes and a conspicuous yellow one, also transverse, occurs on the pronotum; the scutellum is reddish brown.

Duration of Periods Between Molts. The intervals or periods between molts (stages or stadia) in *Colladonus montanus* and the total nymphal stages are given in table 4. The average total duration of the nymphal stages of the males reared on healthy celery was 26.3 days and on infected celery, 27.0 days; and of the females reared on healthy celery, 27.6 days, and on infected celery, 29.7 days. The data show no significant differences in the duration of the nymphal stages between leafhoppers reared on healthy celery and those reared on diseased celery. The total duration of the nymphal stages is shorter for the males than for the females.

Four males reared on healthy celery passed through 6 molts; all other males and females molted 5 times.

Two Species Do Not Interbreed. Since the mottled nymphal instars (plate 1, lower section) of *Colladonus montanus* somewhat resemble those of *C. geminatus* (plate 2, upper section), an attempt was made to interbreed or cross the adults of the two leafhopper species. After the last molt 2 males and 2 lots of 25 males of *C. montanus* reared from mottled nymphs were confined in cages with the same number of female *C. geminatus* reared from mottled nymphs. The reverse cross was made with corresponding numbers of female *C. montanus* and male *C. geminatus*. A similar test was made with male and female *C. montanus* reared from mottled nymphs and kept in cages with adult *C. geminatus* reared from black-banded nymphs. No nymphs appeared in any of the cages. The males of the two species attempted to mate, but the females either kicked the males away or walked away themselves. The two species of leafhoppers did not interbreed.

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