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Effect of Weather on *Cochliomyia americana* and a Review of Methods and Economic Applications of the Study

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This article, which is a review of part of the work begun by the author about 1916 to determine the effects of weather and climate on insect activities and populations, may be of general interest in studies of insect populations, control, and abatement.

METHODS AND EQUIPMENT.—Uniform methods and equipment were developed for all procedures. From variables obtained in the use of these uniform procedures, factors affecting the development, activity, and populations of the screwworm fly were determined, as well as from variables discovered in developing the procedures. This will be discussed further under the separate heads of procedure.

PROCEDURE IN STUDYING WEATHER FACTORS.—Since the Weather Bureau had established uniform procedures for making weather records and had recorded climatic data for the entire United States, these procedures and records were used in the screwworm studies. The basic guide in climatic and weather studies has been the work of Baker (1936).

The subject in hand is basically the reaction of the screwworm to low temperatures. Air temperatures have two regularly recurring cycles—diurnal and annual. Both these cycles complete more or less regular undulations of temperature. The extremes, high and low, of each daily undulation are measured and the mean and the extremes of these daily undulations are the basis for measuring the annual undulations. Over a period of years, daily mean temperature variations are greater than monthly, and monthly are greater than annual variations. In most parts of the United States temperature changes are rather similar at any one time in localities within a radius of 40 to 500 miles or more.

Temperatures at any place will almost certainly fall within the range of extremes established for that place over a period of 20 or more years. The author has used this hypothesis as a basis for applying Weather Bureau data to studies of insect populations and development. After the response of an insect to temperatures is established for an area, other affecting factors being more or less constant over considerable time periods, insect activity within the area can be predicted with some degree of certainty from temperature and other weather trends.

ESTABLISHING FLY-POPULATION TRENDS.—The method of establishing the trend of the screwworm fly population was developed over a 20-year period. The first methods used were counts of flies at carcasses and on wounds, observations of fly infestation in livestock, and miscellaneous trappings. The present uniform trapping method was established in 1931. Results obtained from these uniform trappings coordinated well with weather records for the several species of blowflies. Although the weather and fly populations over areas with radii of approximately 40 miles or more coordinated for each trapping period, it was found that the catches varied greatly as between traps only a few feet apart when the traps were in different environments. A uniform trap environment was therefore established.

Notwithstanding this care in the placement of traps, the trapping results still did not coordinate well with case incidence and severity of screwworm attack on livestock, and this discrepancy was found to be due to the confusion of *Cochliomyia macellaria* (F.) with the closely related but then undetermined species *C. americana* established by Cushing & Patton in 1933. In 1935, characters were found by which rapid and accurate field determinations could be made of the primary screwworm fly, *C. americana* in both adult and larval stages. Since that year the numbers of screwworm flies taken in traps have been determined to be good indices to case incidence and severity of attacks of this fly on livestock in any area.

In the present trapping method use is made of standard cone traps (18 inches in diameter and 24 inches high), each baited with 2 pounds of beef liver in 5 quarts of water in an enameled bait pan. The baited traps are usually set from 20 to 40 or more miles apart and in ecological environments representative of the region. When thus spaced there are from 2 to 10 or more traps in each area of a particular ecological and weather type. The findings from these traps are checked by reported incidence of cases in livestock for each area. The traps are serviced twice each month, usually near the fifteenth and the last day of the month. One man usually services about 30 traps in a circuit of from 500 to 1000 miles, and records the fly catch. When less than 5 quarts of flies are taken in a trap, the number of primary screwworm flies included is determined from an actual count. When a trap contains more than 5 quarts of flies, the total number of primary screwworm flies present is estimated from the number counted in a 5-quart sample. When no primary screwworm flies are found in a 5-quart sample, the entire catch is examined to determine the presence or absence of the fly.

FLY ACTIVITY, HABITS, AND DEVELOPMENT.—*Cloth Cages.* Cages were constructed of tobacco shade cloth stretched over light wood frames and were of any desired size. They were first used in studies of the tobacco budworm, *Heliothis virescens* (F.), in Florida in 1913 and have been used since for studies of several other insects. They were located in an environment suited to development of the screwworm fly, and as nearly natural conditions as feasible were simulated in them. Each cage was stocked with a known number of any desired stage or stages and was continued in use from generation to generation of the insect or for any desired period. The purpose in the use of these cages was to study, under as nearly natural conditions as feasible, the development, habits, and continuity of a fly population. The results obtained in the cages were confirmed by field studies. The cages used in the overwintering studies of the screwworm fly were 12 feet on each side and from 6 to 7 feet high. The frame was made of 1-by-2-inch strips fastened to a continuous base of 1-by-12-inch boards set 6 inches in the soil. The cages were set over pasture soil with as many native plants inside as possible, and food and host material were supplied for all insect stages. The fly activities in the cages were fairly comparable with those in the field.

Field Recovery Cages. The cages used for field recoveries were made with sides of 1-by-12-inch boards and were 3 feet square and covered with 16-mesh metal cloth. The board frame base was set 6 inches deep in the soil. These cages were used to determine the developmental period and percentage of adult emergence from mature larvae dropped naturally or planted on different soil types and soil covers—stony, sandy, or clay soils; cultivated or pasture lands; and bare or with grass, manure, leaf, or other cover as might be found in areas in which studies were made. From 100 to 500 mature larvae were planted in each cage setting. The cages were set up at the cessation of fly activity in the field and again during the cool season when fly activity in the field was indicated during the warmer periods.

Metal-Cloth Cages. Other, cylindrical cages were constructed of 16-mesh metal cloth and were 2 feet high and 10 inches in diameter with a removable top or a small, cone-trap top of wire screen. They were used to cover mature larvae or newly formed pupae planted at regular intervals during the cool season. The larvae were dropped on top of the soil in the cage and the pupae were buried 2, 6, 10, and 20 inches in the soil so that information might be obtained as to outcome when larvae are dropped from wounded animals in shallow animal burrows. Usually 50 to 100 of either larvae or pupae were planted in each cage.

Cave and Animal Burrows. Throughout the parts of the United States infested by the screwworm fly many caverns and caves are found. Some of these are several miles long and extend hundreds of feet below the surface of the earth. Most of the area is also infested by burrowing animals of several species susceptible to attacks of the screwworm fly. Larvae and pupae of the fly were planted in these caves and burrows at intervals during the cool season, and observations were made to determine whether the screwworm flies visited or inhabited these caves and burrows during winter months.

ASSEMBLING AND COMPUTING DATA.[1]—The data presented have been taken from original notes and from manuscripts filed at Uvalde, Tex., and Tempe, Ariz., which include also summaries of reports and manuscripts giving data from other laboratories. All the experiments were executed from a work outline prepared by the author of this section, and all methods and equipment were the same as those used at Uvalde, with some slight modifications to permit the use of equipment available at other laboratories. The basis of this summary has been the observed and recorded reaction of many millions of flies. Several thousand pages of tabulated data have been consulted, and more thousands of tables, charts, and graphs of data have been prepared. As far as possible, discrepancies in data were traced back to the original notes, and incomplete and conflicting data have been eliminated. These summaries are based on the condensed extremes and means of totals in the original records, in so far as it was feasible to determine or present them.

Data have been computed on a monthly basis as far as feasible for the reason that the recorded weather data had been summarized on that basis. The yearly cycle has been used as beginning with the first of any month. Practically all data have been reduced to a uniform scale of 100 units between extremes (Parman 1940).

DISCUSSION OF DATA.—Table 1 presents average daily mean temperatures and rainfall on a monthly basis and indicates whether *Cochliomyia americana* overwintered each year at the several laboratories.

These data indicate that the average daily mean temperature determined whether or not *Cochliomyia americana* overwintered each year at each place, and fixed the determining daily mean averages for the period December, January, and February at near 49° F. as the minimum limit for overwintering. The lowest mean temperature during these months at which the fly overwintered was 49.2° and the highest mean temperature at which they did not overwinter was 50.3°. The daily mean temperature marking the survival limit for the 5-month period was fixed at near 53° F., as the lowest mean temperature at which they overwintered was 53.3° and the highest mean temperature at which they did not overwinter was 53.8°. A study of all data at hand indicates that the populations of the fly usually decrease when the monthly average of the daily mean falls below 60°, other factors being more or less favorable.

No instance has been found in any area in the United States where the fly remained continually present in which the annual average of the monthly means of temperature was below 67° F. For shorter periods than 3 months the average daily mean temperature is not so reliable as an index to the trends of the fly populations and activity, and shorter periods than this are necessarily studied as nonrecurring shock factors.

More than 200 other factors have been found to limit or totally exterminate populations of *Cochliomyia americana*. In the data presented, none of these factors are indicated to have materially affected the statement as to whether some individuals of the fly overwintered, but some of these factors are noticeably operative on the percentage of the population that overwinters.

The average trend of populations of *Cochliomyia americana* during the cool period of 7 years at Uvalde, Tex., as de-

[1] Data have been collected at laboratories of the Bureau of Entomology and Plant Quarantine and by employees of this Bureau as follows: Uvalde, Tex., D. C. Parman, R. A. Roberts, Ralph Conner, A. W. Lindquist, C. C. Deonier, R. W. Burgess, H. M. Brundrett, W. L. Barrett, Jr., E. E. Lester; Tempe, Ariz., C. C. Deonier; Sonora, Tex., O. G. Babcock; Menard, Tex., H. E. Parish; Dallas, Tex., E. W. Laake, Roy Melvin, Raymond Bushland, C. L. Smith; Valdosta, Ga., and Gainesville, Fla., A. L. Brody and E. E. Rogers.

Table 1.—Weather data of various places in relation to winter activity of *Cochliomyia americana*.

Place and Year	Nov.	Dec.	Jan.	Feb.	Mar.	Average Nov.–Mar.	Average Dec.–Feb.	Lowest Temp.	Date	Overwintered
Gainesville, Fla.										
1935–1936										
Mean temperature..	65.5	50.2	56.9	57.0	64.0	58.7	54.7	23	Dec. 21	Yes
Rainfall...........	0.67	1.97	3.97	7.88	2.78	3.46	4.61			
1936–1937										
Mean temperature..	61.6	59.5	58.8	58.7	61.2	59.9	59.0	26	Nov. 28	Yes
Rainfall...........	0.10	2.63	3.32	4.60	3.03	2.74	3.52			
1937–1938										
Mean temperature..	60.5	55.8	56.6	62.8	69.5	61.0	58.4	20	Dec. 7	Yes
Rainfall...........	3.88	1.76	1.90	2.24	1.38	2.23	1.97			
1938–1939										
Mean temperature..	65.9	56.0	59.1	65.5	67.0	62.7	60.2	26	Nov. 28	Yes
Rainfall...........	0.74	0.53	1.84	5.70	1.01	1.96	2.69			
Valdosta, Ga.										
1935–1936										
Mean temperature..	59.5	45.7	51.5	50.4	59.4	53.3	49.2	20	Dec. 27	Yes
Rainfall...........	0.75	1.64	5.45	4.97	2.15	2.99	4.02			
1936–1937										
Mean temperature..	56.9	54.2	64.4	55.3	57.2	57.6	58.0	23	Nov. 28	Yes
Rainfall...........	0.10	5.43	1.04	3.85	5.72	3.23	3.44			
1937–1938										
Mean temperature..	56.6	51.0	52.5	60.1	65.9	57.2	54.5	17	Dec. 7	Only in cage
Rainfall...........	3.73	1.37	1.37	.87	1.95	1.86	1.20			
1938–1939										
Mean temperature..	61.7	51.5	57.3	62.1	64.1	59.3	57.0	22	Feb. 24	Yes
Rainfall...........	1.05	2.44	3.18	6.92	1.60	3.04	4.2			
Dallas, Tex.										
1934–1935										
Mean temperature..	59.6	48.4	49.2	49.5	62.4	53.8	49.0	8	Jan. 21	No
Rainfall...........	5.01	.88	3.33	2.16	0.74	2.42	2.12			
1935–1936										
Mean temperature..	51.8	44.8	43.8	42.0	62.6	49.0	43.5	10	Feb. 18	No
Rainfall...........	1.67	0.90	0.48	0.28	0.90	0.85	0.55			
1936–1937										
Mean temperature..	52.2	50.3	41.9	49.0	51.2	48.9	47.1	19	Jan. 9	No
Rainfall...........	0.74	2.17	1.50	0.28	4.51	1.84	1.32			
1937–1938										
Mean temperature..	52.4	46.5	48.8	54.2	63.8	53.1	49.8	19	Jan. 31	No
Rainfall...........	4.56	5.40	6.34	4.73	4.40	5.09	5.49			
1938–1939										
Mean temperature..	54.1	48.1	50.7	45.6	59.6	51.6	48.1	18	Feb. 21	No
Rainfall...........	1.14	1.00	2.75	4.35	2.49	2.35	2.90			
Menard, Tex.										
1935–1936										
Mean temperature..	53.7	46.7	43.9	48.0	59.9	50.4	46.2	18	Feb. 18	No
Rainfall...........	1.0	1.1	0.2	0.2	0.4	0.6	0.5			
1936–1937										
Mean temperature..	50.8	48.6	43.4	47.5	50.5	48.2	46.5	15	Jan. 23	No
Rainfall...........	0.8	0.9	0	0.3	1.4	0.7	0.4			
1937–1938										
Mean temperature..	56.4	46.2	48.9	48.1	63.5	52.6	47.7	20	Jan. 31	No
Rainfall...........	1.2	4.9	2.1	1.8	0.3	2.1	2.9			
1938–1939										
Mean temperature..	51.7	46.2	49.3	47.8	61.2	51.2	47.8	16	Feb. 10	No
Rainfall...........	0.4	1.7	2.5	0.3	0.9	1.2	1.5			
Sonora, Tex.										
1935–1936										
Mean temperature..	56.8	48.4	47.2	50.0	61.2	52.7	48.5	18	Feb. 18	No
Rainfall...........	0.5	1.2	0.4	0.1	0.8	0.6	0.6			
1936–1937										
Mean temperature..	51.6	51.0	47.8	52.2	54.2	51.4	50.3	16	Jan. 23	No
Rainfall...........	0.5	0.7	0.2	0.3	0.4	0.4	0.4			
Uvalde, Tex.										
1935–1936										
Mean temperature..	60.1	52.6	50.6	53.6	65.1	56.4	52.3	19	Jan. 19	Yes
Rainfall...........	0.3	2.0	0.3	0.1	1.6	1.0	1.1			
1936–1937										
Mean temperature..	57.5	54.5	52.0	57.0	58.0	55.8	54.5	28	Dec. 15	Yes
Rainfall...........	1.1	0.5	0.9	0.1	1.5	0.8	0.5			
1937–1938										
Mean temperature..	59.5	52.0	54.0	60.0	68.5	58.8	55.3	22	Nov. 20	Yes
Rainfall...........	0.2	6.0	2.1	0.7	1.7	2.1	2.9			
1938–1939										
Mean temperature..	59.5	54.5	54.0	53.5	66.0	57.5	54.0	25	Nov. 8	Yes
Rainfall...........	0.0	1.2	1.5	0.3	0.2	0.6	1.0			
1939–1940										
Mean temperature..	57.5	55.0	43.9	53.5	62.9	54.6	50.8	17	Jan. 19	Yes
Rainfall...........	2.0	1.1	0.1	2.3	1.4	1.4	1.2			
1940–1941										
Mean temperature..	59.0	56.8	55.6	53.7	56.5	56.3	55.4	27	Nov. 15	Yes
Rainfall...........	2.3	3.6	1.1	3.9	3.8	2.9	2.9			
1941–1942										
Mean temperature..	59.9	54.3	51.0	54.0	61.7	56.2	53.1	20	Jan. 11	Yes
Rainfall...........	0.5	0.4	0.2	1.3	0.2	0.5	0.6			
Tempe, Ariz.										
1936–1937										
Mean temperature..	59.1	51.0	41.6	52.8	57.8	52.5	48.5	20	Jan. 22	No
Rainfall...........	0.6	2.3	1.6	0.7	2.2	1.5	1.5			
1937–1938										
Mean temperature..	57.5	54.1	52.7	54.6	57.4	55.3	53.8	28	Jan. 111	Yes
Rainfall...........	0.0	0.8	0.4	0.8	0.9	0.6	0.7			

termined by trap catches for each month, is, for October, 291; November, 65; December, 130; January, 75; February, 5; March, 6; and April, 95. Attention is called to the marked decrease of adult flies taken in November. The reason for this is the very marked drop in temperature from a daily mean 20-year average of 72.4° F. for October to a 59.0° average for November. At Uvalde the maximum change was in 1938, when the daily mean temperature for October, 74.0°, dropped to 59.5° F. in November, and the trapped adults dropped from 187 in October to 4 in November. The minimum change was in 1936, from 66.0° in October to 57.5° in November, and the adult fly catch dropped from 156 to 135.

Adult life is short—about 2 weeks—when the daily mean temperature is above 70° F., and the shock of cold nights following warm days kills a high percentage of the population. Adults surviving these shocks and adults emerging during cooler periods live for longer periods in the cool season—about 1 month or longer. The pupal stage is about 10 days at 75°, 15 days at 70°, and 30 days at 60°, with the duration about 20 per cent longer or shorter when influenced by other ecological factors. Normally there is an almost complete cessation of emergence early in November, and the pupal period then extends over into some warm period in December or January.

In order that the effect of factors such as rainfall and temperature on the populations of the screwworm fly may be better studied, table 2 presents the daily mean temperatures for Uvalde, Tex., and Tempe, Ariz., for the 5-month period November to March for different years, these being arranged in the order of increasing temperature, the ratio of adult flies taken in November and December to those taken in February and March in status traps, and the average monthly rainfall at Uvalde and Tempe.

Line No. 1 (Table 2) is eliminated from any study of overwintering, as the fly did not overwinter in any part of Arizona (or in California) during that season. From lines 2 to 6 the average daily mean temperature for the 5-months' period increased from 54.6° to 56.3° F. in steps of approximately 0.5 degree, excepting between lines 5 and 6. Lines 5 to 7 have nearly the same average daily mean temperature, but they have the extremes of winter survival. The ratio of carry-over in the Uvalde trap (line 5) was 83:0; in 5 other traps plus the Uvalde trap the ratio was 76:1. These three lines also have the extremes and near mean of the rainfall presented in table 2. While the extreme low rainfall of line 5 is near that of line 3, the data for line 3 are from a large area of irrigated pastures, whereas line-5 data are from a non-irrigated area. In 1938–39 there was a very low overwintering of the fly in the vicinity of Uvalde. A 5-months' period with 0.5 inch of rainfall per month is indicated as near the minimum rainfall limit of toleration for the fly.

With the higher extreme of rainfall, 2.9 inches per month, the survival was very low, but in line 9 with 2.1 inches per month it was near the highest carry-over and survival was also recorded at Gainesville, Fla., and Valdosta, Ga., with over 3 inches of rainfall per month. The factor of type of rainfall was probably operative. The rainfall for the period in line 6 was slow, misty, and continuous. The same type of rainfall prevailed for the month of December in line 9, but rain was inter-

Table 2.—Degree of reduction of *Cochliomyia americana* populations during winter and effect of the rainfall factor: Five-month period November to March, inclusive, at Tempe, Ariz., and Uvalde, Tex.

Line No.	Place	Year	Nov.–March Temperature (°F.) Daily mean	Min.	Flies Taken in Traps Nov.	Dec.	Jan.	Feb.	Mar.	Flies Taken in Trap Nov.–Dec.	Ratio of Flies Taken in Nov. and Dec. to Those Taken in Feb. and Mar.	Average Monthly Rainfall (Inches)
1	Tempe	1936–37	52.5	20	62	13	0	0	0	75	75:0	1.5
2	Uvalde	1939–40	54.6	17	94	364	14	6	2	458	57:1	1.4
3	Tempe	1937–38	55.3	28	49	18	3	2	2	67	17:1	0.6
4	Uvalde	1936–37	55.8	28	135	214	178	24	4	349	12:1	0.8
5	Uvalde	1941–42	56.2	20	80	3	5	0	0	83(304)[1]	83:0(76:1)[1]	0.5
6	Uvalde	1940–41	56.3	27	29	209	79	1	1	238	119:1	2.9
7	Uvalde	1935–36	56.4	19	12	111	237	3	18	123	6:1	1.0
8	Uvalde	1938–39	57.5	25	4	12	1	0	0	16	16:0	0.6
9	Uvalde	1937–38	58.8	22	101	0	14	0	14	101	7:1	2.1

[1] Six traps in Uvalde area.

mittent in the other months. This is reflected in the trap catch of December (line 9) instead of the usual increase over that of November. This will be discussed later in the overwintering of different stages of the fly.

When the data are charted and extended on an annual-cycle basis for the Uvalde type of climate and weather, the limits of tolerance of *Cochliomyia americana* to rainfall are indicated as approximately a minimum of 0.4 inch and a maximum of 5 inches per month. The highest annual populations have developed when the monthly average rainfalls were between 1.5 and 3 inches per month.

Many other factors affecting the overwintering of the fly are reflected in the data presented. The more important of these are the numbers of the fly at the beginning of the winter period, the type of host material, and temperature and rainfall types rather than averages. Most of these factors were operative for short periods and to a great extent were lost in averages.

WINTER HABITS AND ACTIVITIES.—There are many factors that affect the day-to-day development, habits, and activity of the several stages of the fly. Little or no coordination of development or activity with any of these factors can be shown for these short periods, although the extremes which cause total arrest of development or activity may be determined. Toleration limits for the fly must be established before preventive or control measures are undertaken or attempts are made to change population trends over longer periods.

HABITS OF ADULTS.—The adult screwworm flies have never been observed to seek protection from cold either while in cages or under natural conditions. They usually rest on low vegetative growths or other objects from near the ground to about 10 feet high, some drop to the ground when the air temperature falls below freezing, and all have usually dropped by the time 20° F. is reached. Some fallen flies will revive and begin to show life if the temperature rises to 45° within a few hours, and they will crawl or fly back to their perches when the temperature reaches 50° to 55° if factors are favorable.

Feeding and normal life activities begin at approximately 60° F. Few flies revive after being subjected to temperatures of 20° and none have survived from lower temperatures. The percentage of dropped flies making normal recovery rises from approximately 1 per cent or less at exposure to 20° to 90 per cent at 32°. As has been stated, abrupt and sudden changes in temperature are usually fatal to a high percentage of the adults. Such temperature changes are frequent in the Southwest, the daily range being as much as 70 degrees or more. Daily ranges of as much as 40 to 50 degrees markedly shorten the life of the adult when minimum temperatures are below 30° F.

Adults are normally inactive at night. Normal activity begins soon after sunrise and ends shortly after sunset. They seek the lightest areas in cases and usually the brightest sunshine under natural conditions, except at high temperatures, when they seek light shade. They are less active on cloudy days and become inactive with heavy clouds. They have never been found resting in buildings, caves, burrows, or any deep shade; but they do visit these places to oviposit, and natural oviposition has taken place in the almost complete darkness of a small coop in a goat shed on a bright, hot day. The flies will enter rather heavily shaded areas to some extent to feed. For these reasons the trends of the screwworm fly population may tend to be higher in areas or during winters with a high percentage of sunshine than in places or times with less sunshine. (See Uvalde data, table 2, lines 6 and 7. The period covered by line 6 had 38 clear days and that by line 7 had 76 clear days.)

Adult fly activity is retarded by winds of 5 or 6 miles per hour and is prevented by winds as high as 15 miles per hour. For this reason more adults are taken in traps in brush areas than on prairies or open plains. The fly does not inhabit heavy, dense forests. Other factors being equal, the areas with highest overwintering ratios are rolling to rugged, and brush covered. Catches in traps located one above another indicate that the adults are more active near the ground and do not enter traps in the tops of the highest brush cover. The ratios at Uvalde were approximately as follows: On ground, 50 adults; 4 feet above, 10; and 12 feet above ground, 2. At 18 feet above ground none were taken in mesquite trees approximately 25 feet high. Charts recording average wind movements on areas where the screwworm fly occurs throughout the year show the effect of wind on its over-wintering. Valleys and brush cover provide windbreaks to a considerable extent, especially near the ground. Adults are seen and are taken in traps in open areas on days with little wind movement. During winter periods small, open, sunny areas usually have more active adults than brush areas.

Rainfall and moisture affect the adult markedly. Adults are inactive during continuously rainy periods. Referring to the record for Uvalde, for December, 1937 (Table 1), no adults were taken in the status trap during the month, and yet a nearly normal population was indicated in the preceding month. No heavy rains fell during the month until December 29, when a fall of 2.27 inches was recorded, but there was almost continual slow, misty rain on 25 other days of the month. Compare these data with those of December 1935 at Uvalde, 11 days with rainfall in two distinct periods, and those of December 1936 at Tempe, Ariz. (Table 1).

In the cloth cages at Uvalde adults lived through December 1937 to January 18, 1938, but were inactive practically all the month of December and no oviposition was obtained during the month, although adults of all ages were in the cage at the beginning of the month. The first recorded oviposition and cases of attack in the field were on January 14, 1938, and only a few additional cases were noted during the next 6 days. This will be discussed further under the subject of pupae.

The adults appear to have their longest life span during cool, moist weather. The maximum life span for an adult, 76 days, was recorded during the winter of 1940–41 at Uvalde. Rather long life spans were recorded at Gainesville, Fla., and one of 61 days at Valdosta, Ga., in 1936–37. Adults confined in a cage without water in some form rarely live more than 2 or 3 hours when temperatures are above 80° F., and not more than 2 or 3 days at the lowest temperatures not lethal to the fly. Moisture also is advantageous in keeping the food supply available. When baits in traps become dry they are not attractive to *Cochliomyia americana*. Animal-carcass baits kept immersed in water have remained attractive more than 6 months. The adults are apparently able to use condensed moisture transpired by plants, or possibly hygroscopic moisture, to maintain life. Adult populations decrease rapidly as plants in an area reach the permanent wilt stage. During extremely dry winters the populations of the fly are maintained only near streams and about stock-watering places.

Adults are always most abundant in areas used by livestock. In some of the desert areas in Arizona, lying between the higher mountain summer grazing lands and the large irrigated valleys used for winter grazing and feeding, the fly was taken only at the time bands of sheep were being moved through these areas in fall or spring.

Adults require a live, warm-blooded animal with a wound or diseased tissue for natural oviposition. With one exception the fly has never been observed to oviposit under natural conditions on other tissue; the exception was an adult that laid its eggs on the head of a sheep about 2 hours after the sheep had been slaughtered and when the air temperature was high. In the laboratory, at high temperatures, well-fed, mature, adult females readily deposit normal masses of eggs on lean meats and other media. In animals subject to attack of the fly, only about 5 per cent as many natural wounds occur in the cool seasons as in the warmer months.

As with many other insect pests, man has provided this insect with hosts and the conditions necessary to build up its numbers, by providing these in abundance during the most critical part of its annual cycle. More than 90 per cent of winter infestations of screwworms are in avoidable man-made wounds in livestock and wild animals (Parman 1941). During the winter months the fly, being less active than during other seasons, requires more readily available host materials for reproduction and survival than when higher temperatures prevail. For this reason a critically low population at the beginning of the winter may not survive. (See table 1, Uvalde 1938–39 and 1941–42.)

CONDITIONS AFFECTING THE EGGS AND LARVAE.—As a rule low temperatures do not materially affect the egg and larval stages of the fly. The egg stage may be slightly prolonged by cold, and in extreme cases of cold rainy weather incubation is prevented. The normal incubation period is approximately 8 hours, and this period is rarely prolonged to more than 24 hours.

The larvae penetrate more deeply into the wounds during cold periods, and larvae dropping during cool weather tend to penetrate more deeply into the soil. In warm weather they pupate from under very slight cover to more than 2 inches deep. As cooler weather approaches they penetrate hard soils 1 or 2 inches and loose soils to 6 inches or more. Larvae dropping at air temperatures below 40° F. soon become immobile, and unless the soil is warmer than the air they usually pupate or die on the surface of the soil. Larvae dropping at temperatures between 15° and 20° F. usually die. The normal larval stage is from 4 to 10 days, with an average of about 6. The larval stage of the fly can endure 10 days of any low temperatures not fatal to the host.

CONDITIONS AFFECTING THE PUPAE.—The pupal stage of the screwworm fly is affected by innumerable factors, for the reason that under natural conditions the stage is located in diverse environments and has no capacity of choosing or of relocating to better its environment. The best that can be done in this discussion is to give the general effects of varied environments and state some specific cases and results.

Temperature is the controlling factor in the developmental period of the pupae. When mean daily air temperatures drop below 60° F., other factors begin to become more effective in influencing the temperature of the immediate site of the pupa and its development both as to time and percentage of emergence of adults. Pupae held at fairly constant temperatures near 55° rarely produce adults. The lower the moisture content of the media, the higher the percentage of emergence at average daily mean air temperatures between 50° and 60°.

During the winter of 1935–36, characterized by reasonably dry, sunshiny weather, approximately 40 per cent of the larvae introduced into the cages late in November produced adults in from 22 to 45 days. Adults fed and were active in December, both in the cloth cage and in the field, but there was no oviposition until the middle of January, when a rather severe outbreak of screwworm cases occurred in the field.

During the winter of 1937–38, however, which was a wet season, there was no emergence from the larvae or pupae planted late in November, but adults from the October and early November introductions lived to January 18, although they were inactive and fed little. No oviposition was indicated in the field or in cages in December, and only a very few screwworm cases were found in the field from January 14 to 20, 1938.

The lowest average daily mean air temperature at which the pupae have produced adults from larvae on dry range soil was 47.6° F. The lowest air temperature to which pupae have been exposed in dry range soil and produced adults was 17°. They did not survive at 15°. Pupae have rarely survived in frozen soil with a moisture content high enough to freeze the soil solid.

Practically all pupae are in the top 6 inches of the soil, and the temperature of this soil is affected by a multitude of factors such as composition, moisture, sunshine, cover, and exposure. Except when the composition is manure or some material supporting organic combustion to produce heat, soil temperatures follow the trends of air temperatures, and can be quite accurately determined from air temperatures after compensation has been made for the type of soil, exposure, and weather. In a sandy soil with a certain slope, soil temperatures may be taken over a period and these compared with air temperatures during the same period under the different weather types (cloud, sunshine, wind, rainfall, etc.), and this trend of soil temperature may be used in connection with any period of air temperatures.

In table 3 are presented data of soil and air temperatures that indicate trends on the average rolling, brush-covered, sandy-clay soil of southern Texas ranges. These data were obtained near Crystal City, Tex. about 40 miles south of Uvalde. They are for the annual cycle June 1937 to May 1938, with the additional months of November and December 1938, in order that these months may be discussed in connection with the trend of populations.

The temperatures presented in table 3 were taken with thermographs and

Table 3.—Trend of soil temperatures with relation to air temperatures near Crystal City, Tex.

Month and Year	Average and Range of Daily Means: Air temp. (°F.) (monthly) Mean	Range	Soil temp. at 6 inches (°F.) Mean	Range	Soil temp. at 2 feet (°F.) Mean	Range	Soil temp. at 8 feet (°F.) Mean	Range	Absolute: Max. temp. (°F.) Air	Soil at 6 inches	Min. temp. (°F.) Air	Soil at 6 inches	Rainfall (inches)
1937													
June	85.4	26.3	91.8	15.0	88.6	1.1	79.1	1.9	107	104	65	76	3.11
July	84.6	24.0	90.1	16.3	88.7	1.1	80.2	1.4	103	104	68	78	1.28
Aug.	85.5	26.1	92.3	15.4	91.4	1.3	81.9	1.7	110	106	62	74	2.28
Sept.	81.6	20.4	84.1	14.5	86.1	2.2	82.5	1.4	99	103	57	67	8.65
Oct.	67.9	24.8	71.9	13.9	76.6	0.5	81.1	2.1	94	88	46	56	1.62
Nov.	59.4	21.6	60.7	10.7	67.6	0.7	77.2	1.7	92	82	33	49	1.10
Dec.	57.2	24.0	56.4	10.3	62.5	1.3	72.8	1.1	82	68	30	40	0.67
1938													
Jan.	54.4	20.0	53.2	8.8	60.7	1.1	70.0	1.4	85	70	30	41	0.00
Feb.	59.3	28.4	60.0	12.8	63.6	1.3	68.3	2.0	93	77	31	48	0.13
Mar.	62.2	25.0	64.8	13.5	66.9	1.6	68.9	1.8	94	82	31	49	1.33
Apr.	73.2	31.4	76.1	15.0	74.0	1.4	69.8	2.3	104	40	40	56	0.05
May	80.1	26.0	83.0	14.2	81.9	0.8	73.8	2.0	98	96	57	67	3.41
Nov.	61.4	27.6	63.8	13.2	69.9	1.4	80.2	2.0	90	84	27	42	0.86
Dec.	55.0	15.7	52.8	9.7	59.0	1.5	74.7	1.5	77	64	32	42	4.69

the air temperatures were checked with self-recording maximum and minimum thermometers. The data are presented for the use of a reader not acquainted with the trends of soil to air temperatures. They will not be discussed further than to call attention to the effect of rainfall on the trend of soil temperatures in relation to air temperature, especially for the months of November and December 1938.[1]

The temperatures on the surface of bare soils have on the average a much greater daily range than air temperatures. Soils in deep caves and caverns have almost constant annual temperatures, usually from 1 to 5 Fahrenheit degrees above the average mean of annual air temperature.

Caverns, animal burrows, and manure accumulations have never been indicated to be effective in extending the overwintering area of the fly into areas with 3- or 5-month periods of air temperatures below the determined limits of average overwintering temperatures. The percentage of those surviving the winter may have been increased, but, if so, such increase has not been determined to be significant.

There is evidence that animals infested in southern Texas with screwworms and shipped to northern states in late winter and early spring take with them to the northern sales pens mature larvae which are dropped there. These larvae and pupae receive protection from cold that would be lethal on pasture lands, and by the time adults emerge, temperatures are high enough for development and reproduction.

When cold prolongs the pupal stage to more than 40 days the percentage of adults emerging drops rapidly, and rarely more than 1 or 2 per cent emerge after a 50-day period. One of the longest pupal periods ever recorded was from December 12, 1939, to February 27, 1940, 77 days, at Uvalde. In this test larvae had been planted on range soil and emergence began on February 8, 1940, after a period of 58 days with average daily mean air temperature of 47.6° F. The average air temperature from January 16 to 31 was 39°, the mean maximum 52.1°, the mean minimum 26.0°, and the absolute minimum was 17°. The lowest soil temperature recorded was 32°. Nineteen per cent of the pupae produced adults. A pupal period of from 28 to 78 days was reported at Valdosta, Ga., in 1935–36, from the carcass of a goat. A maximum pupal stage of 70 days was obtained from larvae planted in manure, and a maximum of 65 days on range soil and on cultivated soil at Tempe, Ariz., 1937–38.

Moisture does not appear to affect the developmental period of the pupae to a marked degree, but it does affect to a marked degree the percentage of adults emerging from the pupae. As has been stated, pupae withstand the greatest cold in dry media, and as the percentage of the water in the medium increases to the point of saturation the percentage of adults emerging from pupae decreases to zero regardless of the temperature. The

[1] It is the author's opinion that a standardized procedure of taking soil temperatures in several regions of diverse environment for long periods of time would materially advance economic entomology and insect-pest prevention and control.

fly rarely establishes or develops a population in any area with more than 5 inches of rainfall per month and in no area with a slow, continuous type of rainfall above 4 inches per month. In table 1, Valdosta, Ga., data of 1937–38, it is indicated that the fly overwintered in cages, but not in the field. The probable reason was that the fly population had decreased to the critical population point before November, as the 4 months preceding had rainfall as follows: July, 7.32 inches; August, 5.86 inches; September, 6.21 inches, and October, 4.64 inches. The last case of screwworm attack observed in the field was on November 10, 1937, and no other case was observed until June 16, 1938.

At Dallas, Tex., in 1937–38, Laake & Smith used a cloth cage covered with tarpaulin. The earth floor was covered with 6 inches of straw, mixed with cow, goat, and sheep manure, and goats and sheep were kept in the cage. Larvae were planted in the cage as follows: 2000 in November 8–11, 200 in December 20–22, and 3000 in January 10–15. One female emerged January 27 and there was continuous emergence to February 15, totaling 53 females and 33 males. Intermittent emergence continued to May 3 from these larvae, and larvae dropped subsequently. No oviposition was observed or indicated either in cages or in the field.

LIFE SPAN OF A GENERATION.—Experiments in cloth cages to determine the total period from oviposition to the death of the last adult of a population indicates that for a winter generation at Uvalde the period is rarely more than 3 months and is usually about 2.5 months or less. The longest period was that obtained in 1940–41 from 100 larvae, reared in a goat and planted in a screen-cylinder cage, the adults from which were kept in the field in a small wire-screen cage with sugar and water available at all times. Oviposition was observed on November 4, and the larvae dropped from the wound and were planted on range soil November 11. Emergence began December 12 and continued to December 19, when the entire number had emerged. One male and one female lived to February 14, 1941, when the last male died; the last female was dead March 6 and probably died March 5. The total period was 121 days. Allowing 10 days for the egg and larval stages and adding the longest pupal period (78 days) and the longest adult life recorded (76 days), a total period of 164 days would be obtained. From observations, trappings, and cage experiments no such period is indicated in the field. The effective, maximum-generation span in nature is probably less than 100 days.

ECONOMIC PHASE OF DATA.—In areas from 80 to 1000 miles wide and for periods of more than 3 months, the average of weather trends follows the same patterns, and trends of the screwworm fly populations tend to follow weather-trend patterns, other factors remaining constant, for the same periods. This is especially true of annual cycles, or as indicated in data presented for the overwintering period. These trends shift to some extent from central points over shorter periods, and local differences occur. For some seasons or longer periods weather trends are modified over wider areas because of shifts of the major storm tracts or change in their type, size, etc., from the normal. When these changes develop to the extent that longer periods of cold or extremely cold weather prevail in an area, overwintering of the fly is prohibited, as at Tempe, Ariz., in 1936–37. When the weather changes are less, the degree of overwintering of the fly is affected, as at Uvalde.

Livestock management remains more or less fixed in all areas over long periods. Its procedures become established because of climate, lay and use of land, financial customs, etc. Since any radical changes in livestock management might seriously affect the entire economy of the area, any proposed changes should be as slight as possible, should be made gradually and with the cooperation of all concerned, and should affect the fewest possible industries, so that losses to individuals and to the livestock industry may be prevented.

As has been stated, man frequently makes conditions favorable for the development of insect populations. As an example, the sheep and goat industry of southwestern Texas did not have so great a screwworm problem as long as flocks were herded and watched. The labor and predatory-animal factors in sheep and goat production became acute, and animal-proof fences were developed in a rugged, brush-covered grazing area. Sheep released in large ranges of this area would often not be found and treated after receiving injuries, and consequently high populations of the screwworm fly were built up.

It was found that the highest populations in this area followed a rather long shearing period at a time of the year most favorable to the development of the fly in shear-cut wounds. Sheep and goats are sheared twice each year—spring and fall—in the area, and each period lasts 3 to 4 months. From data at hand it was indicated that high populations of the fly would be prevented to a great extent by shortening the shearing period as much as feasible and making it come slightly earlier in the season. No serious objections were encountered to this program, and in January 1941 it was generally recommended as a part of the ranch management to prevent screwworm attack.

Shearing earlier in the fall season prevented a high population of the fly from carrying over to December and January. Creating a wound-free period from October 1 to January 31 decreased chances for development of a generation of the fly to carry over to spring. This has apparently been reflected in the fly populations, as determined in traps during the winter of 1941–42. A survey as of May 1, 1942, indicated that from 5 to 90 per cent of the sheep owners and all goat owners are complying with the program in the various counties in the area.

Comparable methods have been found advantageous in developing preventive measures for eye gnats, *Hippelates* spp., the sticktight flea, *Echidnophaga gallinacea* Westw., and the fowl tick, *Argas miniatus* Koch. Area distribution and its determining factors have been worked out for several species of blowflies and their parasites and predators. As has been indicated in this review of the ecology of the primary screwworm fly, temperature is the limiting factor in the distribution of all insects, and many other factors either limit or prohibit the distributions of an insect within the area to which the insect is limited by temperature conditions.

SUMMARY.—The normal overwintering of *Cochliomyia americana* is confined by climate to the extreme southern parts of the United States. The adult fly has no well defined resting stage, but development and activity are retarded during cooler months.

Tests of the overwintering of this fly in the states of Florida, Georgia, Texas, and Arizona indicated that the average daily mean temperature for 3- and 5-month periods determined whether the fly overwintered in these areas. The minimum temperature limit for the 3-month period was near 49° F. and for the 5-month period was nearly 53°. Most adults are killed when minimum temperatures fall below 20° F. Practically all pupae are destroyed with minimum temperatures below 15° F. Pupae withstand cold better in dry media than in those moist or wet, and the longest pupal period was 78 days. The lowest average daily mean temperature at which pupae survived was 47.6° F. In this case the minimum period covered was 58 days, and emergence continued for a period to total 77 days; the total emergence from this series in dry range soil was 19 per cent.

Other factors limiting the degree of overwintering of the fly were rainfall, hosts, population of fly at beginning of winter, and many lesser factors. Adults live longest during cool, moist periods. The egg and larval stages of the fly usually are not materially affected by weather.

The actual maximum period of carry-over of one generation was 121 days, and the possible carry-over of combined maximum periods of all stages was 164 days.

Caves, animal burrows, or manure accumulations are not indicated to increase the area of overwintering.

The study indicated that shearing at an earlier and not so extended period in the fall would greatly reduce screwworm cases among sheep.—11-17-44.

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