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TECHNICAL MEMORANDUM

METEOROLOGICAL LIMITS ON THE GROWTH AND DEVELOPMENT OF SCREWWORM POPULATIONS

By

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1. INTRODUCTION

The screwworm is the larval stage of the fly *Cochliomyia hominivorax*, Coquerel. The larvae feed only on living tissue forming a parasitic relation with a wide range of wild and domestic animals. Tick bites, wounds left by castration and dehorning, and the navals of newborn animals are common points of infestation. The larvae move in place with a corkscrew motion, hence the name screwworm. Left untreated, crippling or death of the host animal is inevitable.

Screwworm flies at one time were found from Florida to California and as far north as Nebraska. In the late 1800's, many lifestock producers were occasionally forced to restock due to heavy losses caused by the screwworm. Before effective controls, domestic livestock losses were estimated at $20 million annually in the Southeastern United States and $50 to $100 million in the Southwest.

In the early 1950's, researchers with the U.S. Department of Agriculture (USDA) showed that careful irradiation of the pupal stage of the fly produces sexual sterility (ref. 1). The sterile flies continue to mature normally and demonstrate the same types of activity as wild flies. It was noted by researchers that the typical female screwworm mates only once, while the male continues to mate throughout its lifetime. When large numbers of sterile screwworms are introduced into the environment, a sizable portion of the wild female flies mate with sterile males resulting in infertile eggs. Thus, the fly's own reproductive cycle is used to limit its populations.

Efforts to completely eradicate screwworm populations through animal husbandry practices seem to have failed because wild animal populations maintain a screwworm population which can reinfest domestic animals. In 1955, it was estimated that 50 to 90 percent of the screwworm flies in Texas were produced by wild animals. More recent estimates place this figure much lower. Even so, if only 20 percent of an existing screwworm population reproduce, the next generation will be the same size as the parent generation. Thus, a program such as the USDA sterile male drops, which affect the entire reproductive population, is the only approach which can hope to eradicate the screwworm. The sterile-male program has clearly resulted in a sharp reduction in the number of screwworm infestations in both the United States and Mexico (ref. 2), yet a number of puzzling outbreaks have occurred.

An excellent survey of the research leading to the USDA program for screwworm eradication is given in reference 3. More detailed information may be found in references 4 and 5.

In 1973, the Health Applications Office at The National Aeronautics and Space Administration, Lyndon B. Johnson Space Center (NASA/JSC) began a program to evaluate the use of remotely sensed data as an additional tool in existing and projected eradication efforts. The need to relate remotely sensed data to screwworm infestations resulted in a two-part developmental study. First, the ability to use remotely sensed data to estimate weather conditions was evaluated. Second, the effect of weather on screwworm populations was modeled. Barnes and Forsberg (ref. 6) have provided an excellent overview of the program's approach. This report deals with the salient points of the weather-population interaction.

2. ROLE OF WEATHER IN SCREWWORM GROWTH AND SURVIVAL

That weather conditions, particularly soil moisture and air temperature, influence the growth and survival of screwworm populations has been recognized for a number of years (ref. 7). Meteorological extremes have served to limit the distribution of screwworm infestations. In fact, the unusually cold winter of 1957-58 has been credited with a large contributory role in the successful effort to eradicate screwworms from the Southeast (ref. 8). Currently, the screwworm is restricted to tropical and subtropical areas of North and South America during the winter months, with large populations overwintering each year in Mexico. Each summer, as temperatures increase, screwworm flies advance from Mexico into the United States and remain until cool temperatures prevail. Figure 2-1 shows the total number of screwworm infestations reported in Texas, by month, since the beginning of the eradication program in 1962. Of particular interest are the outbreaks occurring in 1968 and 1972. These outbreaks have, at least in part, been attributed to favorable weather conditions.

As a point of departure, an extensive literature review of the effect of selected environmental conditions on the growth and development of the screwworm was undertaken (ref. 9). Based on that study, it was recognized that a wide range of meteorological parameters can affect fly activity including air and soil temperatures, precipitation, sky cover, humidity, windspeed, and soil moisture. In addition to meteorological conditions, there are a number of other important factors which influence fly populations: availability of hosts, predators, incidence of wounds, topography, condition and type of vegetation, and the effects of the eradication program itself.

All of these concomitant factors can and do play a role in the observed fluctuations of screwworm populations. However, until recently, there has been no real way to quantify the effect of a given set of weather conditions on screwworm populations. Historically, attempts to relate weather conditions to the number of screwworm infestations, while producing mixed results, have

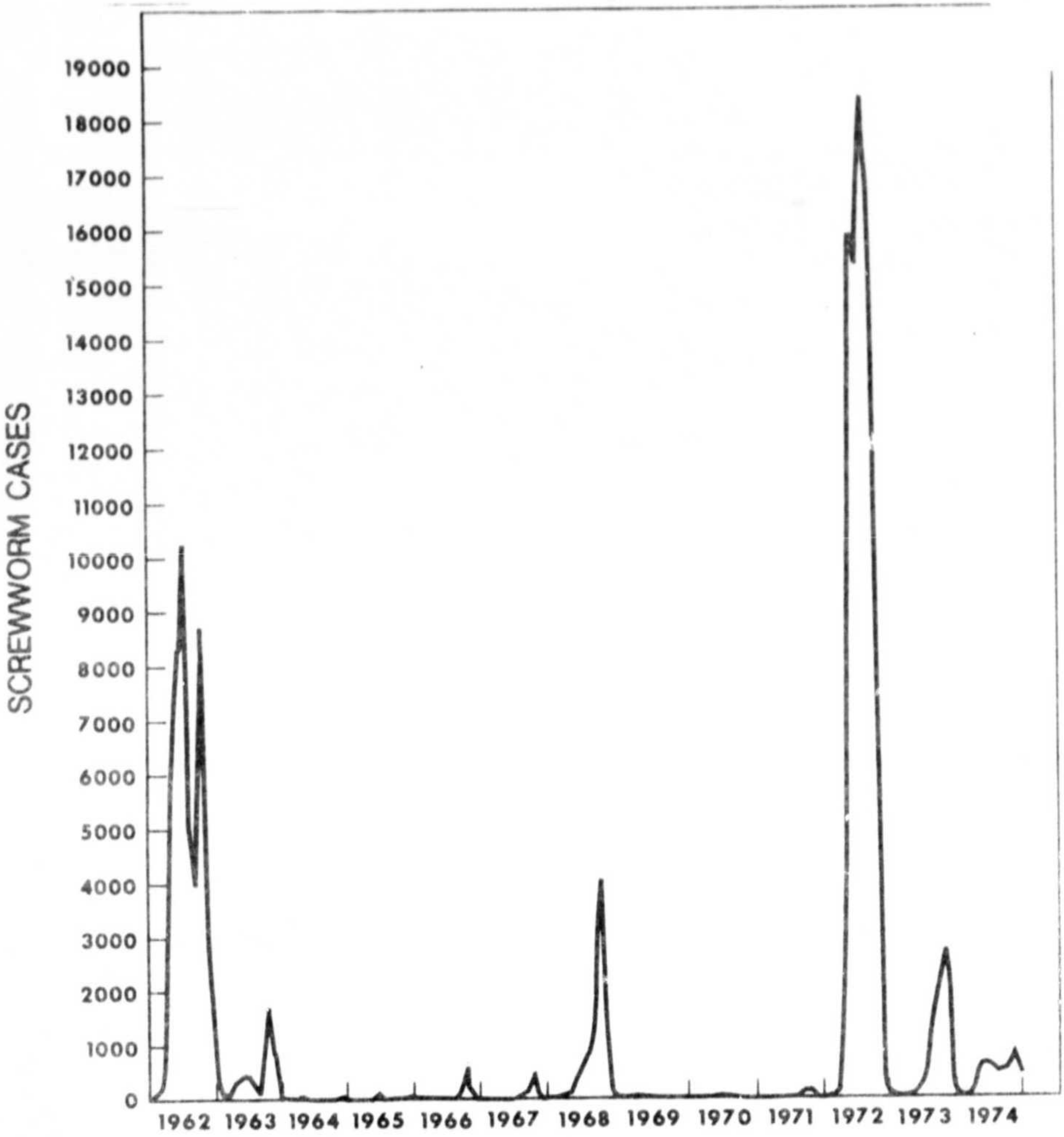

Figure 2-1.— Monthly screwworm cases for Texas.

clearly identified air temperature and soil moisture conditions as important parameters (ref. 10). The problem then is to quantify the effects of a given set of meteorological conditions such that standard statistical techniques can be used to analyze weather-screwworm relationships.

2.1 SOIL MOISTURE AND AIR TEMPERATURE

As might be expected, the nature of the available data shaped the basic study of weather-screwworm relationships. Data on several of the desirable parameters were either completely unavailable or available only at prohibitive cost.

Based upon the literature survey and upon a number of preliminary statistical studies, it was decided to concentrate on the effects of soil moisture and air temperature.

Soil-moisture data based upon direct measurement are extremely limited and generally unavailable. The use of a moisture-budget approach, utilizing more commonly measured meteorological variables, has been suggested by a number of authors. The approach using conventional measurements of air temperature and precipitation (ref. 11) was extended to provide a measure of long-term moisture anomalies (ref. 12).

In 1968, a related measure of short-term moisture anomalies was also developed (ref. 12). This parameter, called the Crop Moisture Index (CMI), has come into general usage and is published weekly during the summer in the *Weekly Weather and Crop Bulletin* of the U.S. Department of Commerce. The CMI varies around zero. When positive, the index indicates a surplus of moisture and conversely a deficit when negative.

The CMI is calculated on a weekly basis for each climatological division in the United States. These divisions are multicounty areas considered to be fairly homogeneous both climatologically and hydrologically. The 10 climatological divisions for Texas are shown in figure 2-2.

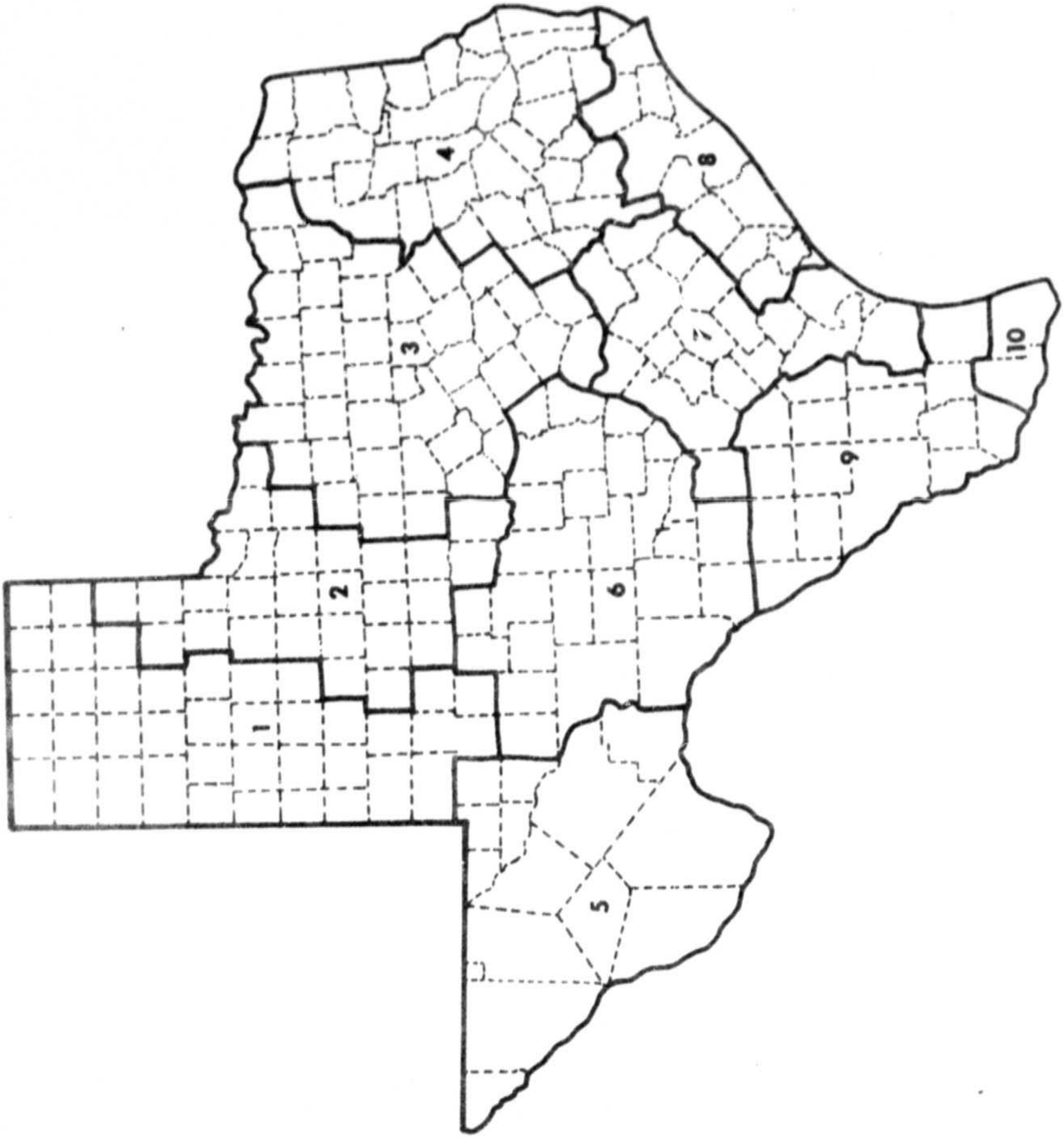

Figure 2-2.— Texas climatogical divisions.

The meteorological data base for this study consisted of weekly values of mean air temperature, total precipitation, and CMI for each climatological division in the Southwestern United States. These values represent the average of data from all meteorological stations in the division.

The basic infestation data were taken from weekly Agricultural Research Science summaries by county for the years 1967-73. The data were further summarized into weekly total infestations for each climatological division.

The study of environmental influence on the screwworm is complicated by several factors. First, data on the number of cases are based primarily on rancher reports of infected livestock. These reports may be delayed for various reasons, and some cases may never be reported. When and how often cases "occur" is partly a function of how frequently a rancher checks his herds, a factor controlled partly by previously reported cases in his area. Thus, a type of "feedback" exists, where a greater percentage of actual cases is likely to be reported during a serious outbreak than during a time when screwworm activity is low.

An additional complication is the eradication program itself, which holds down the amount of screwworm activity that might otherwise occur under a given set of environmental conditions. Because of the nature of the eradication program, it is not possible to completely separate the variation due to program from that due to environmental parameters.

2.2 METHODOLOGY DEVELOPED TO DETERMINE WEATHER INFLUENCE ON SCREWWORM GROWTH AND SURVIVAL

Based upon data obtained from the literature survey and the screwworm's life cycle as shown in figure 2-3, a sample model was developed to examine the influence of weather on screwworm growth and survival. This model was used to calculate the average weather and resulting growth per generation for several years of historical data in the Southwestern United States.

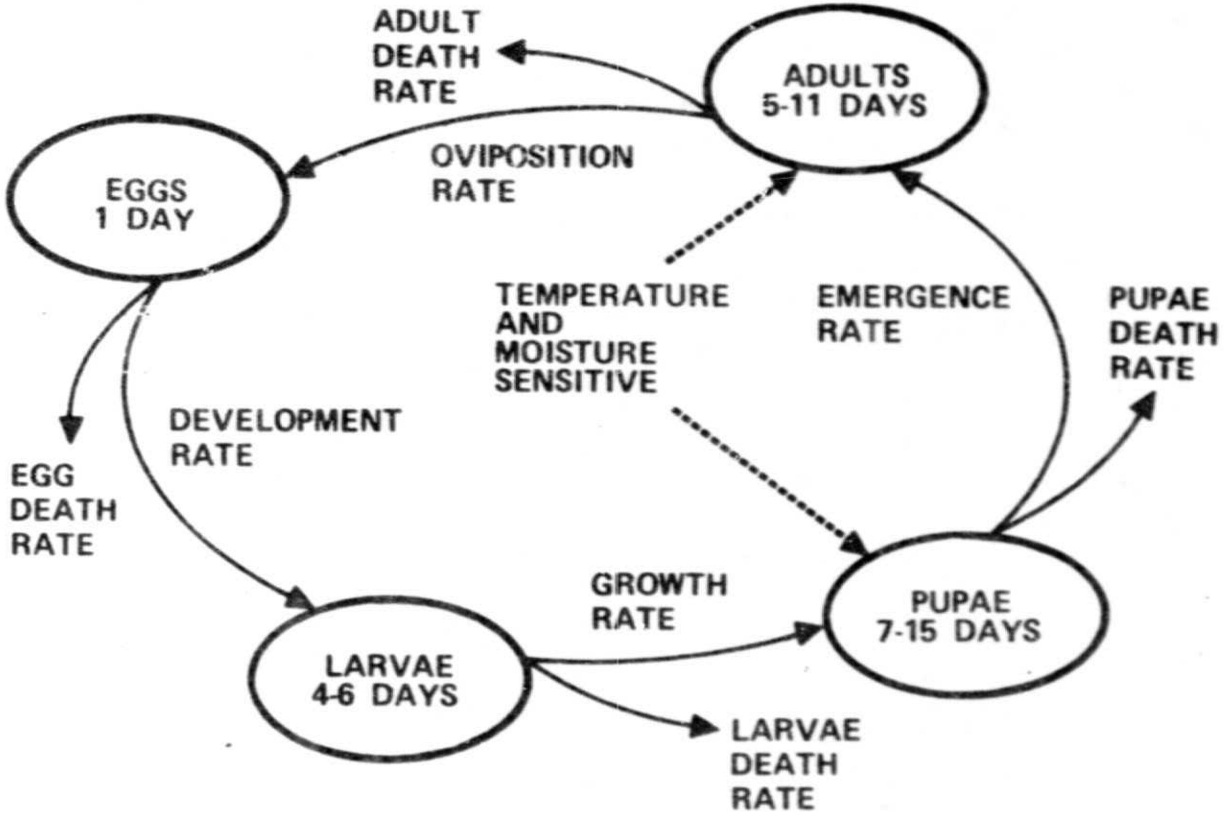

Figure 2-3.— Idealized diagram of the screwworm life cycle.

The growth per generation was defined as the ratio of the number of cases during a given week to the number of cases reported during the week in which the parent generation occurred. The length of time between the parent and progeny generation was determined using the average times given for each phase in figure 2-3. The length of the pupal phase, which is temperature dependent, was determined by a degree-day calculation.

Laboratory data on the development time of screwworm pupae at various temperatures are shown in figure 2-4. By converting these developmental times to their reciprocals and extending the resulting line to zero, a developmental threshold value of 10.8° C (51.44° F) was estimated along with a thermal constant of 139.1 degree-days. The length, n, of the pupae phase is the first n which satisfies the following equation

$$\sum_{L=1}^{n} (T_i - 10.8) \leq 139.1$$

where T_i is the daily mean air temperature in °C.

Average conditions of temperature, total precipitation, and CMI value were computed for the adult phase prior to first oviposition and the pupal phase. The weather conditions during each phase were then plotted against the resulting growth per generation.

The plots of weather conditions versus screwworm population growth resulted in the definition of a set of screwworm potential functions. This was accomplished by observing the maximum growth per generation under a wide range of temperature and soil-moisture conditions. For commonly repeated conditions, a wide range of growths was observed. Those growths, less than the potential, can be attributed to a variety of limiting factors including a lack of wounds, natural predators, and effects of the eradication program itself. Some points were observed which represented unexpectedly large growths. These points were attributed to sampling error in some cases and to the migration of flies into areas to take advantage of favorable conditions.

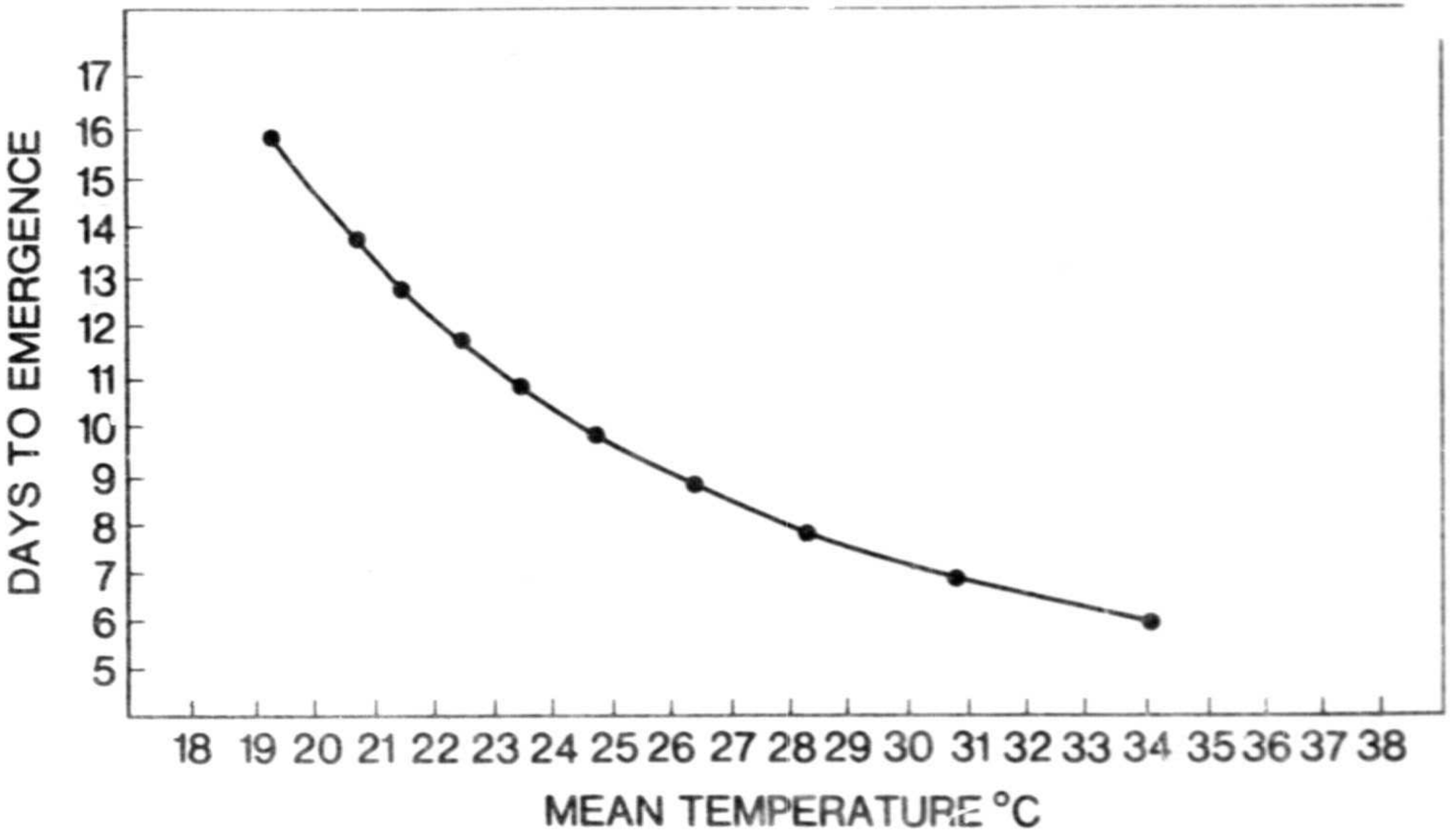

Figure 2-4.— Laboratory data on the development time of screwworm pupae at various temperatures.

Careful analysis of all available data resulted in the weather potential functions given in figures 2-5 and 2-6. These figures are intended to represent the potential growth of a single generation of screwworm, if that meteorological parameter is the *only* factor acting to limit the screwworm population.

The screwworm potential, given as a function of air temperature, has a gradual increase from zero near 10° C (50° F) to a maximum of approximately 27° C (82° F), followed by a sharp decrease around 30° C (85° F).

The screwworm potential as a function of soil moisture increases to a maximum near 0.8 and then falls with increasing moisture. This function represents an empirical verification of laboratory reports showing a lower survival for screwworm pupae under extremes of soil-moisture conditions.

In a similar manner, the screwworm potential as a function of generation length was derived. Shown in figure 2-7, the potential is maximum when the generation length is near 3-1/2 weeks.

To evaluate the potential utility of these growth functions four models were developed. Two models were designed to predict growth per generation, whereas the remaining models predicted actual infestations. Each model was built using the same set of data used to develop the growth functions.

The first model, known as Model 1, is a multiplicative model for growth and the formula follows:

$$G_0 = a_0 x_1^{a_1} x_2^{a_2} x_3^{a_3} x_4^{a_4}$$

where

G_0 – growth per generation

x_1 – growth potential of mean air temperature during the adult phases

x_2 – growth potential of mean air temperature during the pupae phases

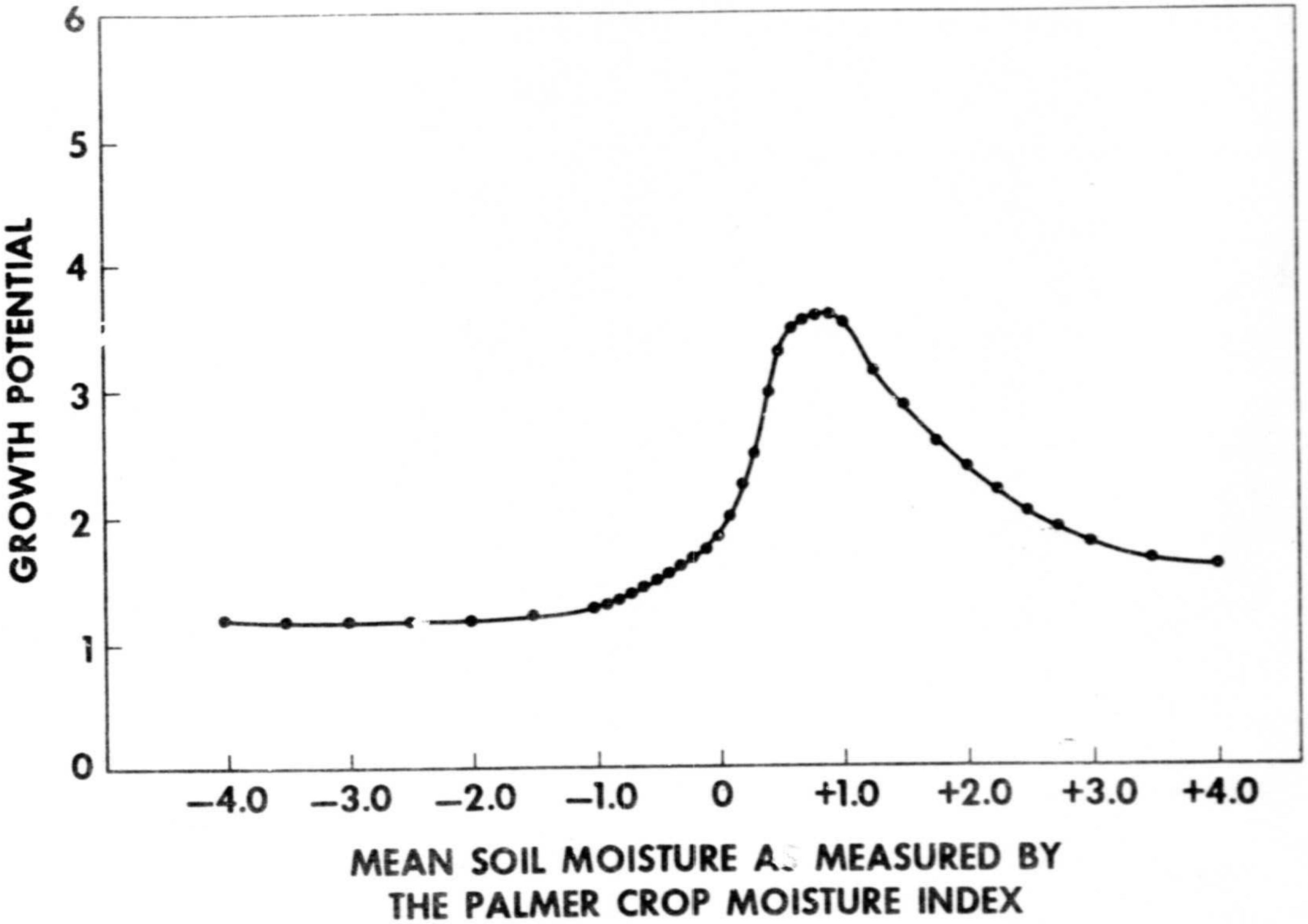

Figure 2-5.— Relationship between CMI and growth per generation.

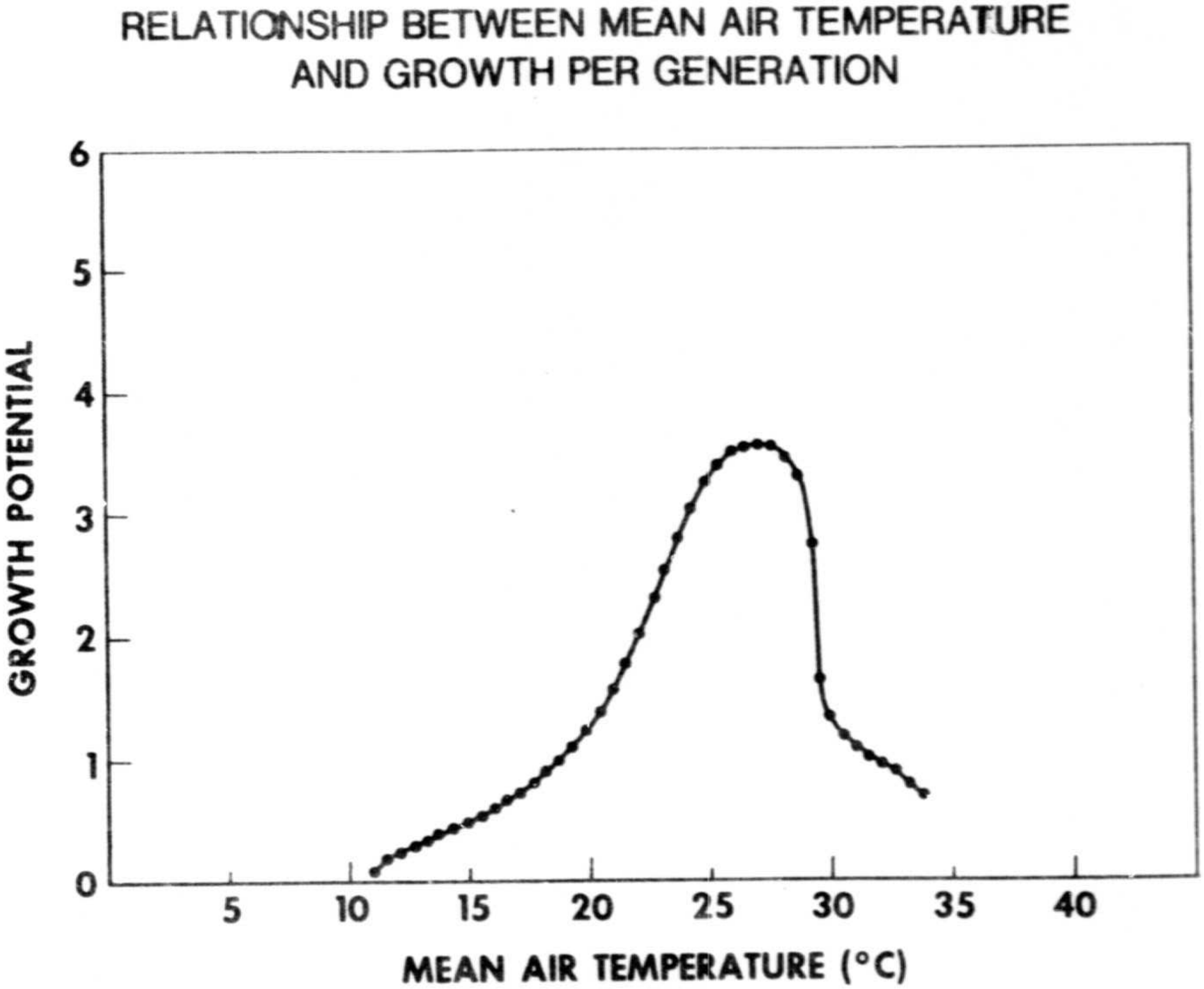

Figure 2-6.— Relationship between mean air temperature and growth per generation.

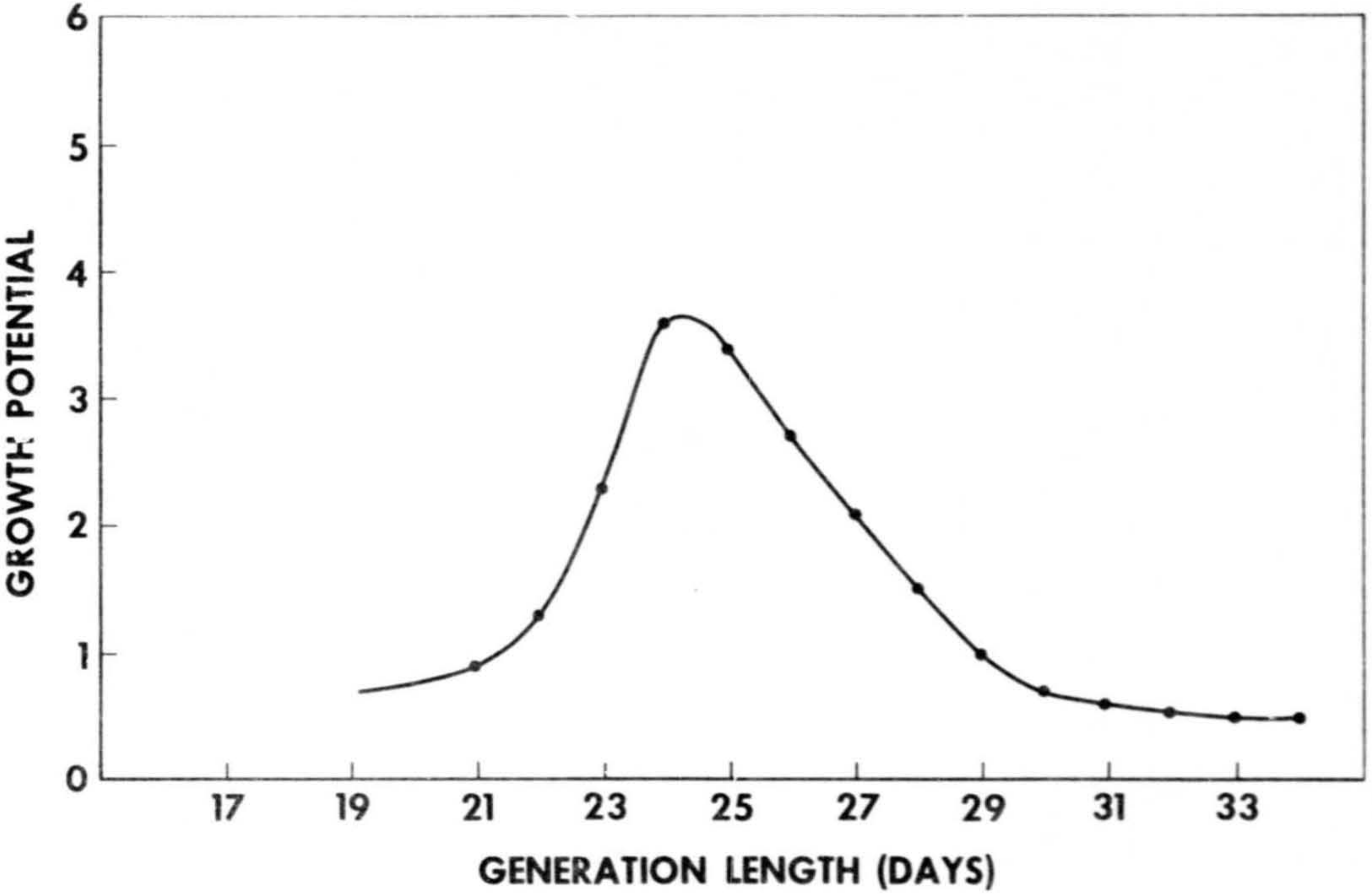

Figure 2-7.— Relationship between generation length and growth per generation.

x_3 – growth potential of CMI

x_4 – growth potential of mean pupation time

The second model includes the infestation, as measured by reported cases, of the parent generation as an additional independent variable. Model 2 may be written:

$$I_o = b_o x_1^{b_1} x_2^{b_2} x_3^{b_3} x_4^{b_4} x_5^{b_5}$$

where

I_o – current infestation

x_5 – infestation during parent generation

The third model adds the actual growth per generation observed 1 week in the past. Model 3 may be written:

$$G_o = c_o x_1^{c_1} x_1^{c_2} x_2^{c_3} x_4^{c_4} x_5^{c_5} x_6^{c_6}$$

where

x_6 – observed growth per generation 1 week in the past

The final model evaluated utility of Model 3 to predict infestation. Model 4 may be written:

$$I_o = d_o + d_1 G_o x_5$$

Each of these models is either linear or implicitly linear. Thus, the models may be fitted through multiple linear regression. Tables 2-1 through 2-4 present a summary of statistics for each model build.

Model 1 predicts the potential growth generation as a function of observed weather conditions. The adjusted multiple correlation coefficient (R) was 0.515 when the model was fitted to the historical data set. The growth

TABLE 2-1.— STATISTICS FOR MODEL 1

(a) Regression coefficient

Variable	Coefficients[*]	Standard error	t-value
x_1	0.32317	0.19940	1.62
x_2	-.17854	.27203	-.66
x_3	.37625	.12131	3.10[†]
x_4	.57293	.19430	2.94[†]
ℓn (constant)	-71.06738	32.67852	

(b) Analysis of variance

Source	Degrees of freedom	Sum of squares	Mean of squares	F-value
Regression	4	233613.09	58403.27	16.34
Residual	166	593292.92	3574.06	
Total	170	826906.01		

[†] Significant at 0.95 level.

[*] Adjusted multiple correlation coefficient: 0.515.

TABLE 2-2.— STATISTICS FOR MODEL 2

(a) Regression coefficient

Variable	Coefficients*	Standard error	t-value
x_1	0.15213	0.21645	0.70
x_2	-.21072	.29138	-.72
x_3	.53777	.13836	3.89[†]
x_4	.79839	.21263	3.75[†]
x_5	.70187	.06839	10.26[†]
ℓn (constant)	.43349	.29920	

(b) Analysis of variance

Source	Degrees of freedom	Sum of squares	Mean of squares	F-value
Regression	5	68.92	13.78	34.70
Residual	163	64.75	.40	
Total	168	133.67		

[†] Significant at 0.95 level.

[*] Adjusted multiple correlation coefficient: 0.708.

TABLE 2-3.— STATISTICS FOR MODEL 3

(a) Regression coefficient

Variable	Coefficients*	Standard error	t-value
x_1	0.01236	0.09462	0.13
x_2	-.16318	.21757	-.75
x_3	.23395	.12736	1.84†
x_4	-.48307	.19035	2.54†
x_5	-.20947	.06269	-3.34†
x_6	-.59515	.07180	8.29†
ℓn (constant)	.432.14	.28467	

(b) Analysis of variance

Source	Degrees of freedom	Sum of squares	Mean of squares	F-value
Regression	6	34.86	5.81	27.24
Residual	117	24.95	.21	
Total	123	59.81		

†Significant at 0.95 level.

*Adjusted multiple correlation coefficient: 0.749.

TABLE 2-4.— STATISTICS FOR MODEL 4

(a) Regression coefficient

Variable	Coefficients*	Standard error	t-value
$I_{-n}G$	1.05758	0.04131	25.60†
Constant	3.82065	5.30875	
x_1	.01236	.09462	.13
x_2	-.16318	.21757	-.75
x_3	.23395	.12736	1.84†
x_4	.48307	.19035	2.54†
x_5	-.20947	.06269	-3.34†
x_6	.59515	.07180	8.29†
ℓn (constant)	.43214	.28467	

(b) Analysis of variance

Source	Degrees of freedom	Sum of squares	Mean of squares	F-value
Regression	1	1126673.88	1126673.88	655.15
Residual	122	209803.89	1719.70	
Total	123	1336477.77		

†Significant at 0.95 level.

*Adjusted correlation coefficient: 0.917.

potential of CMI and the mean pupation time were significant. The growth potential of the short-term mean air temperature was weakly significant. The growth potential of the long-term air temperature was not significant, probably due to the high correlation (0.825) with the growth potential of mean pupation time.

Model 2 adds the parent generation infestation as an independent variable to the set of weather parameters in Model 1. Model 2 also predicts infestation. The adjusted multiple correlation coefficient was 0.708; the growth potentials of short- and long-term mean air temperatures were not significant in this model.

Model 3 adds a sixth independent variable in the form of the observed growth per generation 1 week prior to the prediction time. This model predicts growth per generation. The adjusted multiple correlation coefficient was 0.749. As in Model 2, the growth potentials of short- and long-term mean air temperatures were not significant.

The differences between Model 1 and Model 3 are important and should be clearly understood. Model 1 predicts the potential growth per generation as a function of weather. Thus, a high potential for growth may exist anywhere if weather conditions are favorable. Model 3 predicts actual growth per generation of an existing population. If no screwworms are present in an area at the time of the parent generation, Model 3 will predict no growth.

Model 4 fits the product of the growth predicted by Model 3 and the observed infestation during the parent generation with a simple linear regression to predict infestation. The adjusted multiple correlation coefficient was 0.917. The growth potentials of the short- and long-term mean air temperatures remained nonsignificant due to the high intercorrelation of the three temperature-based terms.

This model has an interesting feature in that, due to the constant term, it will introduce a small (three cases) infestation into an area regardless of the weather conditions. However, the population will never grow unless the condition becomes favorable.

The accuracy of predicted infestations is one measure of the relative effectiveness of these models. Table 2-5 gives the relative performance of each model as measured by the standard error of estimate.

TABLE 2-5.– STANDARD ERROR OF ESTIMATE FOR EACH MODEL

Model	Cases	Mean, %
1	79.1	0.949
2	70.3	.844
3	41.6	.413
4	41.4	.411

Models 2 and 4 are case models and can be evaluated directly. The predicted cases from the growth Models 1 and 3 were calculated by multiplying the predicted growth by the number of cases observed during the parent generation.

3. CONCLUSIONS

Although complete validation of models of this type is difficult and requires extensive field data, it is clear that relatively simple weather-based models can successfully be used. A significant portion of the variation in screwworm population growth and development has been traced to weather-related parameters. Clearly, valuable insights into the complex ecological situation governing screwworm population dynamics are available through simple weather models.

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