A Model of the Flight Phenology of the Beet Armyworm (Lepidoptera: Noctuidae) in Central California

D. B. Hogg and A. P. Gutierrez

A model of the flight phenology of the beet armyworm (*Spodoptera exigua* Hübner) was constructed using a combination of laboratory and field experimentation. The model incorporates the following relationships: 1) developmental rates of immature stages as linear functions of temperature, 2) age-dependent immature mortality rates, 3) age-dependent oviposition rates, 4) age and temperature-dependent adult mortality rates, and 5) adult flight activity as a function of temperature.

The model was used to examine beet armyworm flight phenology by simulating light trap catches. An extensive black light trapping program was conducted at five locations in three climatic regions within central California to provide a total of six data sets for these tests. Results of the simulations were generally favorable. When initialized with early season light trap data, the model was able to predict the patterns subsequently observed for the locations in the San Joaquin and Sacramento valleys, indicating that a good understanding of beet armyworm flight phenology in these regions was incorporated. The model did not reproduce observed patterns of flights in the cool Salinas Valley, however, indicating that one or more of the relationships in the model was not valid under the conditions of this region.

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INTRODUCTION

THE BEET ARMYWORM (BAW), *Spodoptera exigua* (Hübner), is one of numerous polyphagous noctuid species that are secondary pests of various crops in California and elsewhere. This pest and the cabbage looper (CL), *Trichoplusia ni* (Hübner), may reach outbreak proportions in cotton in the San Joaquin Valley of California, when pesticides applied for the primary pest, *Lygus hesperus* (Knight), disrupt the parasites and predator populations which normally keep the noctuid populations in check (Falcon *et al.*, 1968[2]; Falcon *et al.*, 1971; Eveleens, van den Bosch, and Ehler, 1973; Ehler, Eveleens, and van den Bosch, 1973; Ehler, 1977; and Gutierrez *et al.*, 1975). The BAW can also be a primary pest early in the season (e.g., on seedling cotton), but this occurs infrequently.

If rational management strategies are to be developed for the BAW (and other pests), the factors which determine its phenology, population dynamics, and impact on the crop must be understood. The impact of the BAW on cotton growth and yields has been quantitatively assessed (Gutierrez et al., 1975); the role of natural enemies in the population dynamics of the BAW is qualitatively known (Eveleens et al., 1973); and detailed models for specific predators in the cotton ecosystem are currently being developed (R. E. Jones, personal communication).

The major objective of this investigation was to develop a model that explains the role of weather in determining the flight phenology (timing and patterns) of this pest under California conditions. The essence of this study is a detailed understanding of the problem; the model is merely a convenient device for assembling the components and testing our understanding of them. Stinner, Rabb, and Bradley (1974) and Hartstack *et al.* (1976) developed population models for *Heliothis zea* (Boddie) and *H. virescens* (F.) which have many attributes in common with this study.

Distribution and biology of the beet armyworm

Since its introduction into North America during the nineteenth century (Harvey, 1876), the BAW has spread throughout the western and southern regions of the United States. This species is multivoltine, with the number of generations completed in a season being determined by climate. Since the BAW apparently does not hibernate during the winter (Fye and Carranza, 1973), permanent establishment is restricted to areas with winters sufficiently mild to allow survival. However, the well documented

migratory ability of BAW adults (French, 1969) permits the species to invade and become established during favorable periods in areas where overwintering does not occur.

Eggs of the BAW are laid in clusters of up to several hundred eggs each and are covered with a mat of scales from the female's abdomen. The larvae initially feed gregariously, then disperse. The larvae are polyphagous feeders, known to attack more than 35 cultivated crops (Steiner, 1936). There are generally five larval instars, and pupation occurs in a loosely constructed cocoon below the soil surface.

The modeling approach

The approach taken in this study has been to construct a mathematical model containing an understanding of the processes important in determining BAW flight phenology and to then test the model's realism by comparing its predictions with observed patterns of BAW moth flights (as measured by light traps). The model's predictions were obtained through the method of simulation (hence, models of this type are commonly known as simulation models), which is carried out most efficiently using a digital computer (cf. Gilbert *et al.*, 1976).

The use of light traps as the sampling tool for estimating adult BAW population density involved some special considerations. Although light traps are commonly used to provide a relative index of the density of moth populations (Southwood, 1966), the samples generally do not correlate well with populations of the immature stages (Johnson, 1969, but see Hartstack *et al.*, 1971). In this study, however, an attempt was made to couple aerial and ground populations via the simulation model. The adult population was defined as all BAW adults within a given area such that each individual had some measurable probability of being sampled by the light trap and all individuals outside the area had no measurable probability of being sampled. Movement of individuals out of the population (emigration) was assumed to be balanced by movement of individuals into the population (immigration). It should be recognized that the population as defined did not constitute an actual group distinct from other groups (Nicholson, 1957; Reddingius, 1971), nor were the boundaries which delimited the area occupied by the population actually known. The population of immatures was defined as the collection of BAW immatures within the area occupied by the adult population.

In order to predict the patterns of BAW moth flights it was necessary to account for the births and deaths that occurred in the population through time. The terms, birth and death, were used in their broadest sense to include metamorphosis from one life stage to the next; e.g., emergence from the pupa represented the birth of an adult and death of a pupa. Birth and death processes generally occur at age-specific rates, and since the rates at which poikilotherms develop or age is governed largely by temperature, physiological time provides the most realistic scale for expressing age (Hughes, 1962; Gilbert *et al.*, 1976). In this study the day degree (D°) concept, which is based on a linear relationship between temperature and rate of development, was used for both time and age (see Campbell *et al.*, 1975, for the assumptions).

The model was structured so that it realistically mimicked the system under study, including population age structure, application of age-specific birth and death rates, and the dynamics of the system. In concept this represented a time-varying life table (Hughes, 1963; Gilbert *et al.*, 1976), and in its simplest mathematical form the model was structured as a Leslie matrix (Leslie, 1945; Gutierrez, DeMichele, and Wang, 1976).

METHODS

For the most part, data gathered from the following studies were used in the construction and testing of the model:

     1. Temperature-dependent development of immature stages.
     2. Survivorship of immature stages.
     3. Fecundity and survivorship of adults.
     4. Flight phenology of adults.

All of the field experiments, with the exception of the flight phenology (light trapping) studies, were conducted on the El Rico Ranch of the J. G. Boswell Land Company, Corcoran, California.

Temperature-dependent development

Laboratory.—Developmental times were recorded for the immature stages of the BAW at various constant temperatures and at a photoperiod of 16:8 light:dark. For the egg stage, experiments were conducted at 15.6, 16.7, 21.1, 26.7, and 32.2 °C. For the larval and pupal stages, experiments were conducted at 16.7, 21.1, and 26.7 °C, with individuals reared in two-ounce plastic cups provided with a modification of Shorey's pinto bean diet (Shorey and Hale, 1965; Ehler, Eveleens, and van den Bosch, 1973).

Field.—Developmental times were recorded for the immature stages of the BAW in cotton during the summer of 1975. All individuals used in this study were from egg masses laid in the laboratory on waxed paper by field collected adults. Egg masses were cut out of the waxed paper and attached to leaves near the middle of plants in the field (unpublished data of DBH suggested this as the preferred oviposition site). Conditions in these experiments were kept as natural as possible, but two modifications of the environment were made for practicality. To minimize losses due to predation, parasitization, and dispersal, most of the larvae were reared in organdy sleeve cages which covered one branch of a plant. When the larvae were judged to be close to pupation, they were placed in two-ounce plastic cups on artificial diet and placed in the soil. Even with these modifications, problems in obtaining large sample sizes were encountered (see Table 3 in Results), due to generally low survivorship of larvae and disruption by insecticide drift from neighboring fields.

Survivorship

Survivorship of BAW eggs and larvae were estimated in cotton during 1975. In these studies, which were performed in conjunction with the field developmental time experiments, eggs and first instar larvae were placed in the field without a protective sleeve cage. Six such studies were done with the eggs, and one study was conducted with larvae. Census data were collected only at egg hatch and pupation to avoid disrupting the concurrent developmental time experiments.

Fecundity and longevity

Laboratory.—Individual pairs of BAW moths (male and female) were placed in eight-ounce waxed cardboard containers soon after emergence and held at one of several constant temperatures. Experiments were conducted at 15.6, 21.1, and 26.7 °C using adults reared from artificial diet, and at 21.1 °C using moths reared from cotton and alfalfa. All tests were performed at a photoperiod of 16.8 light:dark. Each container was supplied with a crumpled piece of waxed paper for oviposition substrate (Eveleens *et al.* 1973), and a small piece of cotton soaked in 10 percent sucrose solution as food (early tests indicated that both longevity and fecundity were greatly reduced without food). Numbers of eggs laid and survivorship of females were recorded daily.

In addition, measurements of pupal weight and the length of one metathoracic femur were made for each female. A statistical analysis was conducted to determine the extent to which the fecundity of individual females varied with these indices of size.

Field.—Experiments were conducted in field cotton during the summer of 1975 to determine the fecundity and longevity of BAW adults. Newly emerged female moths were placed singly in organdy sleeve cages with one or two males. Each cage enclosed a single plant and was tied at the bottom around the stem. A piece of cotton soaked in 10 percent sucrose solution was placed in each cage for food. Every day the plants were cut off at the base and taken to the laboratory, where the moths were removed and the foliage and cage were thoroughly examined for eggs. The moths were then taken back to the field and caged on new plants. Only partial data were collected from this experiment, because the moths were killed prematurely by insecticide drift from a nearby field.

Flight phenology

To obtain a regional perspective of BAW flight phenology, a light-trapping program was conducted during the summer and fall of 1974 at five locations (Fig. 1)—in the Sacramento Valley (Davis), the San Joaquin Valley (Firebaugh, Corcoran, and Shafter), and the Salinas Valley (Gonzales). Data were also collected during 1975 at Shafter.

Traps used for this survey had 15-watt black lights and were standard size and design (Harding, Hartsock, and Rohwer, 1966). Samples were collected in one-quart or larger jars containing 70 percent ethanol. A cooperator at each location serviced the trap daily. Samples were sorted in the laboratory and the numbers of BAW were recorded by sex.

RESULTS AND DISCUSSION

Model construction

Immature development. Reports of laboratory developmental rates of the immature stages of the BAW have been published by Butler (1966) and Fye and McAda (1972). Although both studies were conducted in Arizona, their results differed considerably. Results of our experiments, using insects from the San Joaquin Valley, are summarized in Table 1. The larval and pupal stages were combined because the larval behavior of burrowing before pupating made it difficult to determine precisely when pupation

Fig. 1. Locations used in the light trapping program: (A) Davis, (B) Firebaugh, (C) Corcoran, (D) Shafter, and (E) Gonzales.

occurred. Data in Table 1 were used to estimate temperature thresholds for development to be used for computation of physiological time. The estimates were obtained by regressing developmental rate (the reciprocal of time) against temperature and determining the x-intercept (see Campbell *et al.*, 1975). Results of the regressions are shown in Table 2. Because of the similarity in developmental thresholds (12.2° and 12.3°C) and for convenience, a common threshold of 12.2°C was chosen for all further analyses.

Estimates of the developmental time (D° > 12.2°C) in the field are shown in Table 3. Ambient field temperatures were used for calculating physiological time, although it is known that temperature is modified within the cotton canopy and for the subterranean pupae (e.g., Fye and Bonhan, 1971). However, any temperature correction for microclimatic effects would not necessarily apply generally (e.g., to hosts other than cotton),

TABLE 1.

DEVELOPMENTAL TIMES (DAYS) FOR IMMATURE STAGES OF THE BEET ARMYWORM
REARED ON ARTIFICIAL DIET AT CONSTANT TEMPERATURES

Stage	Temperature (°C)	N*	Mean	S.D.
Egg	15.6	23	9.1	.40
	16.7	6	7.8	.46
	21.1	40	5.0	.28
	26.7	6	2.9	.19
	32.2	8	1.8	.27
Larva-Pupa	16.7	11	55.0	2.60
	21.1	49	34.1	1.76
	26.7	24	18.8	1.34

* For the eggs, this represents numbers of masses.

TABLE 2.

RESULTS OF REGRESSION ANALYSES OF BEET ARMYWORM DEVELOPMENTAL RATE
AS A FUNCTION OF CONSTANT TEMPERATURES

Stage	Estimates of parameters		Estimated developmental threshold
	Slope	Intercept	
Egg	.0268	−.3305	12.3 °C
Larva + pupa	.0035	−.0426	12.2 °C

hence it is assumed that ambient temperature provides a consistent (albeit biased) indication of the temperature perceived by the insects.

Data in Table 3 indicate a sexual difference in developmental times of larvae and pupae, with the males requiring more day degrees than the females to complete both stages. This trend was reported by Fye and McAda (1972) for the pupae, but not the larvae. Because of this sexual difference, only females will be followed in the model—implicitly assuming that the availability of males for mating is never a limiting resource.

Immature survivorship. A detailed understanding of the survivorship of the immature stages of the BAW was not within the scope of this study. In fact, age-specific survivorship has no bearing on adult phenology, though generation survivorship does influence the trends in moth abundance. Hence only preliminary estimates of egg and larval field survivorship were made and are shown in Table 4. Mortality during the egg stage, virtually all of it observed to be due to predation, averaged 39 percent (i.e., 61% survivorship). However, there was considerable variation in survivorship between experiments (CV = 22%). Larval mortality was estimated to be 98.6 percent (i.e., 1.4% survivorship). Mortality to noctuid larvae such as the BAW and CL has been generally found to be greatest in the early instars and the result again of predation (Ehler, Eveleens, and van den Bosch, 1973; Eveleens, van den Bosch, and Ehler, 1973; Ehler, 1977). Various predator species were observed feeding on the eggs and small larvae of the BAW during the field study, including the nymphs and adults of *Geocoris pallens* Stål and *Orius tristicolor* (White), and the larvae of *Chrysopa carnea* (Stephens), though no attempt was made to estimate age-specific larval mortality. Mortality to the subterranean pupae was not measured and is assumed to be negligible.

TABLE 3.

DEVELOPMENTAL TIMES (D° >12.2 °C) FOR IMMATURE STAGES OF THE BEET ARMYWORM
IN THE FIELD (COTTON AS HOST)

Stage	Sex	N*	Mean	S.D.	T
Egg	—	40	52.2	7.97	
Larva	Male	6	300.0	61.92	1.976
	Female	15	261.1	29.75	(p = .032)
Pupa	Male	6	191.1	19.98	1.854
	Female	15	176.7	14.43	(p = .040)
Total	Male		543.3		
	Female		490.0		

* For the eggs, this represents number of masses.

TABLE 4.

SURVIVORSHIP OF BEET ARMYWORM EGGS AND LARVAE IN COTTON (CORCORAN, 1975)

Stage of development	Inclusive dates	Initial number	Number surviving	Survivorship
Egg	7/11–14	1,001	511	.510
	7/15–18	1,797	1,167	.649
	7/17–20	1,937	1,316	.679
	7/22–25	886	718	.810
	8/13–17	823	350	.425
	8/15–19	1,675	950	.567
Larva	7/18–8/15	1,167	16	.014

A survivorship function (Equation 1) for the eggs and larvae was developed for the model.

$$(1) \qquad Lx_1 = \exp(b \cdot A) \qquad \qquad b < 0$$
$$0 < A \leq 313.3$$

where Lx_1 is survivorship, A is age ($D° > 12.2°C$), and b is an empirical constant, which is estimated for each simulation (see Discussion). This function describes a Type III survivorship curve (Slobodkin, 1961), in which the rate of mortality (represented by the parameter b) does not vary with age. The form this function takes is not important for the flight phenology model, but it will be when, for example, knowledge of larval age structure is necessary for assessing damage to plants or the impact of an insecticide treatment.

Fecundity and adult survivorship. Fecundity can be analyzed according to 1) how many eggs are laid during the life of the female (total fecundity), and 2) when they are laid (oviposition pattern). The latter is more important than the former for the model being developed, since oviposition pattern directly influences timing and, hence, phenology. Total fecundity is a problem of magnitude and is thus somewhat relative, being balanced against immature survivorship. Nevertheless, effort has been made to understand both aspects of fecundity, as well as adult survivorship.

The fecundity and survivorship of laboratory-reared BAW females at three constant temperatures are shown in Table 5. These data indicate that temperature influences longevity, total fecundity, and ovipostion pattern. Total fecundity was greatest and longevity shortest at the highest temperature (26.7°C). Total fecundity was greater at 21.1°C than at 15.6°C, and differences in oviposition pattern were apparent between these two temperatures. Data also indicate that all females required at least a two day preoviposition period (i.e., oviposition did not commence until the third night), regardless of temperature. This is consistent with the findings of Shorey et al. (1968), and is probably a reflection of the time needed for a female to become sexually mature and the discrete nocturnal activity pattern of the moths.

In order to generalize the data presented in Table 5 beyond the specific temperatures used, the age of the females was transformed from days to physiological time. Results of this transformation are shown in Figure 2, with age expressed as day degrees above 10°C. As no method is available for direct estimation of a temperature threshold for oviposition, the value of 10°C was determined by iteration (i.e., different threshold

TABLE 5.

SCHEDULES OF SURVIVORSHIP (l_x) AND FECUNDITY (m_x) OF BEET ARMYWORM FEMALES
AT CONSTANT TEMPERATURES. (MOTHS WERE REARED FROM ARTIFICIAL DIET)

Age	15.6 °C		21.1 °C		26.7 °C	
(days)	l_x	m_x	l_x	m_x	l_x	m_x
0-2.5	1.00	0	1.00	0	1.00	0
3.5	1.00	149.4	1.00	151.0	1.00	520.9
4.5	1.00	172.3	1.00	427.1	1.00	459.3
5.5	1.00	139.9	1.00	264.7	1.00	328.4
6.5	1.00	116.6	1.00	186.0	0.92	185.3
7.5	1.00	106.6	1.00	111.5	0.92	93.0
8.5	1.00	77.2	1.00	87.8	0.69	69.1
9.5	1.00	57.3	1.00	61.3	0.62	42.9
10.5	1.00	60.0	0.92	40.8	0.39	25.8
11.5	0.93	38.8	0.92	27.3	0	0
12.5	0.86	39.1	0.85	18.0		
13.5	0.77	33.5	0.54	13.7		
14.5	0.71	31.7	0.31	11.5		
15.5	0.43	25.5	0.23	11.0		
16.5	0.21	31.7	0.15	17.0		
17.5	0	0	0.08	2.0		
18.5			0	0		
		Σm_x = 1079.6		1430.7		1724.7

temperatures were tried, and the one that produced the closest convergence of the oviposition (*Mx*) curves was chosen). Since the need for at least a two-day preoviposition period appears to be independent of temperature, the aging process was not begun until the third day of adult life.
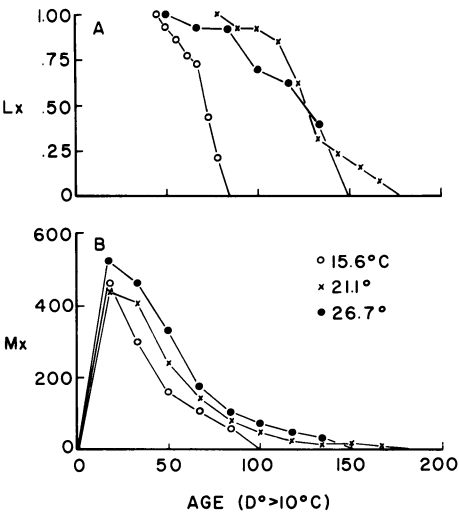

Fig. 2. Patterns of survivorship (Lx), and oviposition (Mx) for beet armyworm adult females at constant temperatures. Moths were reared from artificial diet.
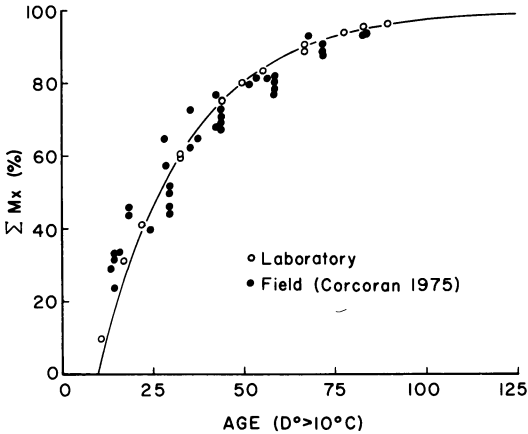

Fig. 3. Cumulative number of eggs laid by beet armyworm moths (ΣMx), scaled as percent of total fecundity, as a function of age. The curve shown is based on the results obtained in the laboratory.

Two major points can be made from Figure 2. The oviposition and survivorship patterns were similar at 21.1 °C and 26.7 °C, with the oviposition curve differing only in magnitude, while at 15.6 °C the oviposition pattern was disrupted and longevity curtailed. The activity of the females was observed to be greatly dampened at 15.6 °C (relative to the other temperatures), perhaps resulting in the moths being unable to feed as frequently as those at the higher temperatures.

A function (Eq. 2) describing the oviposition pattern of the BAW was developed using the data from 21.1 °C and 26.7 °C. The influence of temperature on total fecundity was neutralized by scaling oviposition pattern as a proportion of total fecundity.

$$(2) \qquad \Sigma \; Mx = 1.0 - 1.4734 \cdot \exp \; (-.0402 \cdot A)$$

where $\Sigma \; Mx$ is the cumulative number of eggs laid by a female expressed as a proportion of total fecundity, and A is adult age (D° $>$ 10 °C). This relationship, and the data from which it was derived, are shown in Figure 3. Also shown in Figure 3 are the results of the experiment conducted to estimate BAW oviposition pattern in the field. These field data conform nicely to the laboratory-generated function, providing evidence that this function describes the field oviposition pattern reasonably well.

It has been suggested that temperature can influence the total number of eggs laid by the BAW (Table 5). Detailed analysis of the relationship between total fecundity and (a) temperature, (b) the size of the female, and (c) the host from which the female was reared, were conducted and the results are presented in Appendix A. In short, it was found that total fecundity varies as a function of all three factors. Based on these results, it was estimated that in the field an average BAW female will lay approximately 900 eggs, and this estimate is used for the model.

Survivorship functions for BAW females were developed from the data presented in Table 5 and Figure 2. The first function (Eq. 3) describes age-dependent survivorship.

$$(3) \qquad Lx_2 = \begin{cases} 1.0 & 0 \le A \le 70.9 \\ 1.662 - .009 \cdot A & 70.9 < A \le 178.0 \end{cases}$$

where Lx_2 is survivorship and A is adult age (D° $>$ 10 °C). The second function (Eq. 4) describes temperature-dependent survivorship.

$$(4) \qquad Lx_3 = \begin{cases} 1.0 & 0 \le D \le 10 \\ 2.376 - 0.132 \cdot D & 10 \le D \le 18 \end{cases}$$

where Lx_3 is survivorship and D is adult age (days). This latter function is included in the model to ensure that females do not live for an unreasonably extended period during cool weather but will rarely be invoked during warm periods of the year.

Relationship between temperature and trap catch. Light trap catches provide a relative index of moth abundance which is a function of both the number of moths in the population and the activity level of the moths on the night the sample is taken (Williams, 1940: King and Hind, 1960). Since this model is being developed to simulate trends in light-trap catches, incorporation of some understanding of moth activity is essential.
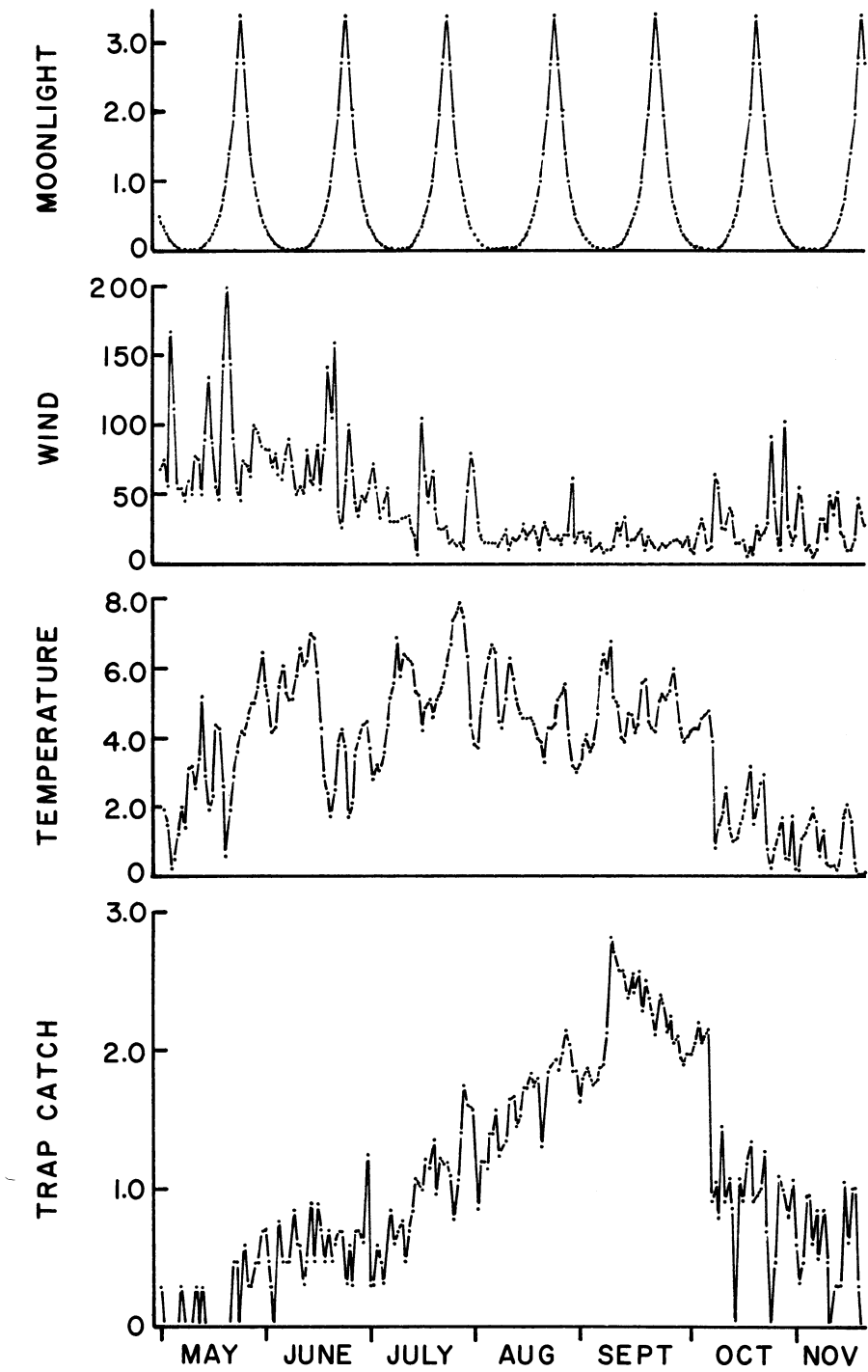
Fig. 4. Patterns of selected physical factors and female beet armyworm light trap catches at Shafter, 1975. Moonlight is expressed as luminance times the proportion of the night above the horizon times 100, wind as miles per day, temperature as night day degrees above 15.6 °C, and trap catch as $\log_{10}$ (number + 1).

Three factors were hypothesized to be important determinants of BAW flight activity in the San Joaquin Valley: night temperature, wind, and moonlight. The patterns of these factors and light trap catches of BAW females at Shafter from May through November of 1975 are shown in Figure 4. Factors such as rain and cloud cover were not included, because they seldom occur during the summer in the San Joaquin Valley. Moonlight was included because of published evidence that it influences light trap catches of *Heliothis zea* (Nemec, 1971; Falcon, 1973; Hartstack *et al.*, 1973).

It appears from Figure 4 that fluctuations in trap catch are correlated with fluctuations in temperature. Moonlight shows no apparent correlation with trap catch. High winds appear to dampen catch, but they occurred infrequently during the summer. Similar results were obtained during 1974 at Shafter. It was decided, therefore, to focus on temperature in an attempt to explain the variation in BAW light trap catch due to activity. Temperature is expressed in Figure 4 as night-day degrees above 15.6 °C—the day degrees recorded from the maximum temperature of the afternoon to the minimum temperature of the following morning. The estimated temperature threshold for flight of 15.6 °C for females of the BAW is based on laboratory observations. The advantage to expressing night temperature in day degrees is that these units provide an indication of both the rate of temperature decline and the activity "time" available to the moths.

The influence of temperature on activity was isolated by examining the relationship between temperature and fluctuations in light trap catch over short periods of time, during which it was assumed that the size of the moth population remained reasonably constant. This approach is similar to that proposed by Williams (1940). The periods surrounding rapid declines in female BAW light trap catch at Shafter in early October of 1974 and 1975 were used, and the results of the analysis are shown in Figure 5. Trap catch in Figure 5 is scaled as a proportion of the largest single night's catch during the respective period (year) and plotted as a function of night-day degrees between 15.6 °C and 32.2 °C. An upper threshold (32.2 °C) was used because there was evidence suggesting an inverse relationship between extreme heat during the day (D °>32.2 °) and subsequent light trap catch. An example of this is shown in Figure 6, which represents data from six consecutive nights at Shafter with similar minimum temperatures. Since this relationship is not well understood, it was approximated by imposing the upper threshold.
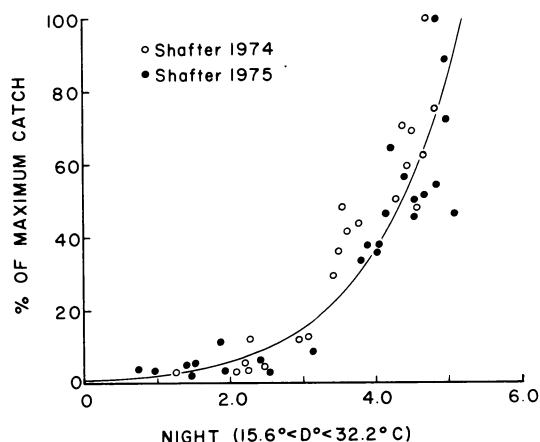

Fig. 5. Influence of night temperatures on female beet armyworm light trap catches (scaled as percent of maximum catch). Data are from Shafter, 9/18 to 10/10/74 and 9/21 to 10/17/75.
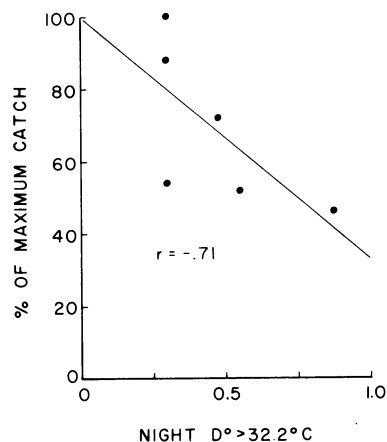
Fig. 6. Relationship between high temperatures and female beet armyworm light trap catches (scaled as percent of maximum catch). Data are from Shafter, 9/21 to 9/26/75.

The curve, which was fit to the data in Figure 5, is described by Equation 5, and this function is used in the model to scale female BAW light trap catch for activity.

(5) $\rho = \exp(0.9032 \cdot X) - 1.0$ $\rho \leq 100$

where ρ is the percent of the maximum potential catch (an activity scalar) and X is night temperature ($15.6° < D° < 32.2°$).

The univariate approach taken in this analysis is not meant to imply that factors other than temperature do not affect BAW flight activity. However, for the summer climate of the San Joaquin Valley the influence of these factors is minimal or absent. Hence an empirical relationship which includes only the influence of temperature can be used to account for much of the variation in light trap catch which is due to activity.

Mathematical structure. The complete BAW model, describing changes in the numbers in each stage and in total numbers during a time step, is summarized by Equations 6–10.

(6)   Eggs:
$$\left[\sum_{a_0}^{a_1} N_i\right]_{t+\Delta t} = \left[\sum_{a_0}^{a_1} (N_i \cdot Lx_1)\right]_t \cdot \Delta t - \left[\sum_{a_1}^{a_1+\Delta a} N_i\right]_{t+\Delta t}$$

$$+ \left[\phi \sum_{a_4}^{a_5} (N_i \cdot F_i)\right]_t \cdot \Delta t$$

(7)   Larvae:
$$\left[\sum_{a_1}^{a_2} N_i\right]_{t+\Delta t} = \left[\sum_{a_1}^{a_2} (N_i \cdot Lx_1)\right]_t \cdot \Delta t + \left[\sum_{a_1}^{a_1+\Delta a} N_i\right]_{t+\Delta t}$$

$$- \left[\sum_{a_2}^{a_2+\Delta a} N_i\right]_{t+\Delta t}$$

(8)   Pupae:
$$\left[\sum_{a_2}^{a_3} N_i\right]_{t+\Delta t} = \left[\sum_{a_2}^{a_3} N_i\right]_t + \left[\sum_{a_2}^{a_2+\Delta a} N_i\right]_{t+\Delta t} - \left[\sum_{a_3}^{a_3+\Delta a} N_i\right]_{t+\Delta t}$$

(9)   Adults:
$$\left[\sum_{a_3}^{a_5} N_i\right]_{t+\Delta t} = \left[\sum_{a_3}^{a_5} (N_i \cdot Lx_2 \cdot Lx_3)\right]_t \cdot \Delta t$$

$$+ \left[\sum_{a_3}^{a_3+\Delta a} N_i\right]_{t+\Delta t}$$

$$(10) \quad \text{Total:} \quad \left[\sum_{a_0}^{a_5} N_i \right]_{t+\Delta t} = \left[\sum_{a_0}^{a_2} (N_i \cdot Lx_1) + \sum_{a_2}^{a_3} N_i \right.$$

$$\left. + \sum_{a_3}^{a_5} (N_i \cdot Lx_2 \cdot Lx_3) + \phi \sum_{a_4}^{a_5} (N_i \cdot F_i) \right]_t \cdot \Delta t$$

where the stage boundaries are
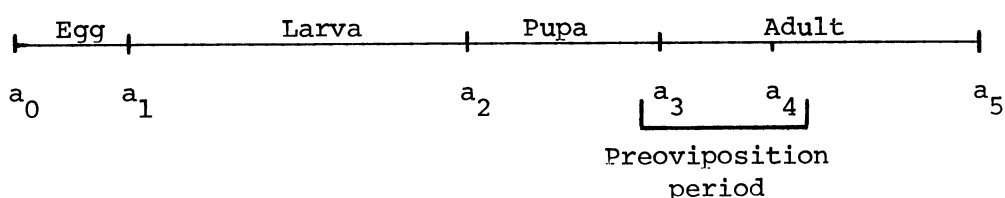
N_i = number of individuals in the ith age category

Lx_1 = age dependent egg and larval survivorship (Eqn. 1)

Lx_2 = age dependent adult survivorship (Eqn. 3)

Lx_3 = temperature dependent adult survivorship (Eqn. 4)

ϕ = correction for adult sex ratio (= .5)

F_i = age dependent oviposition (Eqn. 2)

t = current physiological time

$\Delta t = \Delta a$ = a small increment of physiological time or age

In this study the main interest is in using the model to simulate light trap catches. The model's predicted catch on a given night is described in Equation 11,

$$(11) \qquad N_c = \phi \cdot \rho \cdot \sum_{a_4}^{a_5} N_i$$

where N_c is the number of females caught (hence the correction for sex ratio), and ρ is the temperature dependent activity scalar (Eq. 5).

It is assumed for the model that only ovipositing females are caught, and the probability of a moth being sampled does not change with age. In addition, the light trap is
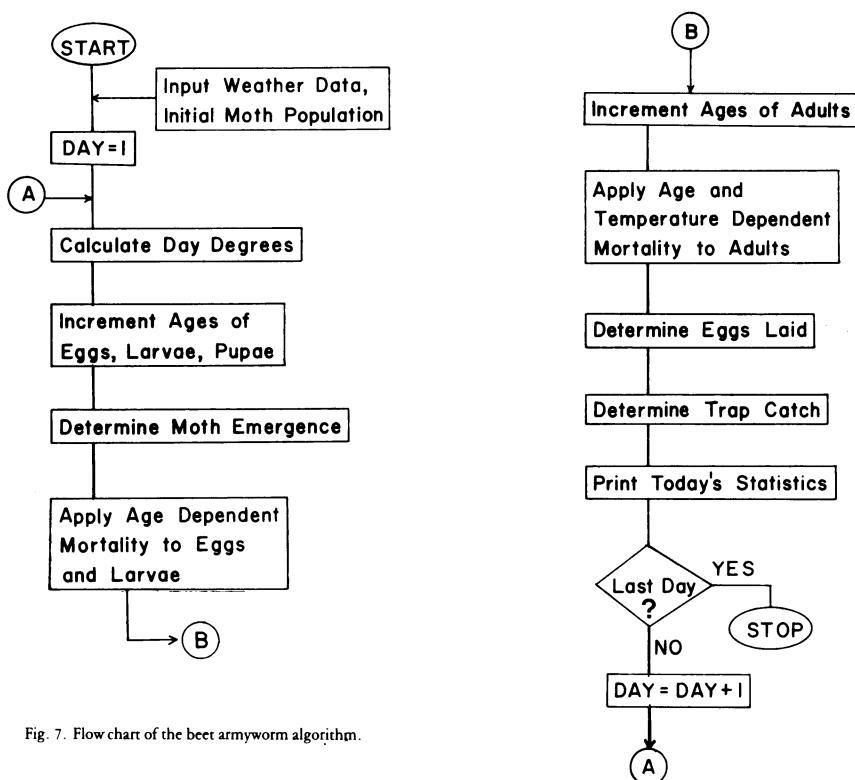
Fig. 7. Flow chart of the beet armyworm algorithm.

assumed to capture a constant proportion of the actual moth population throughout the season, except as this proportion is influenced by temperature.

The components of the model were translated into a Fortran-based algorithm for computer simulation. A flow chart of the algorithm is shown in Figure 7. The simulations are initialized with light trap catches for the period of one generation (i.e., until the first eggs laid have developed into adults), and are driven by weather. The algorithm incorporates a subroutine for determining day degrees (c.f., Gilbert and Gutierrez, 1973), which computes the daily time step from maximum and minimum temperatures. Each day the algorithm increments the ages of all cohorts, applies the appropriate mortality and natality, and determines how many moths will be sampled by the light trap. This process continues until the last specified day of the simulation.

Model testing

The test of a simulation model is the degree to which it mimics data not used in the formulation of the model. The results of these independent tests can be used to assess the model's realism and to point to specific gaps in knowledge. In this study, the model is tested by assessing its ability to reproduce the timing and patterns of BAW moth flights as measured by light traps.

Except for the initial moth data which must be provided, the model's predictions are independent of the observed data, with the following exception: The value of the parameter b (Eq. 1), which determines the rate and overall level of mortality during the egg and larval stages, is estimated from the observed data. This parameter absorbs the effects of (1) the influence of biotic factors (e.g. host effects and predation) which may profoundly influence migration, birth, and death rates in BAW populations, and (2)

the relationship between the location of a light trap (relative to hosts, other lights, and the like) and its sampling efficiency. Hence, b becomes a composite scalar which adjusts at each location for effects not included in the model. The value selected for this scalar in a particular simulation was that which was judged to best match the predicted and the observed catch. Thus, although b was used to align magnitudes, its value remained constant for the duration of that simulation, and it had no influence on patterns.

The model was tested against six sets of data, which included five trapping sites during 1974 and 1975. These sites were located in three climatically different regions: the central to southern San Joaquin Valley (Firebaugh, Corcoran, and Shafter), the Sacramento Valley (Davis), and the Salinas Valley (Gonzales). The physiological time (D° > 12.2 °C) accumulated at each site, the major cultivated hosts of the BAW near each site, and the location and exposure of each trap are compared in Table 6. The San Joaquin Valley, a major cotton producing area, was the warmest, with the Sacramento Valley slightly cooler, and the near coastal Salinas Valley substantially cooler. Smith and Hagen (1965) give an analysis of other aspects of climate for these regions, and Johnston and Dean (1969) present a detailed survey of the cropping patterns in these regions.

Simulation results. Results of simulations conducted for the three locations in the San Joaquin Valley (Figs. 8 to 11) were generally satisfactory. The model's predictions matched best with the data from Corcoran 1974 (Fig. 8), Shafter 1974 (Fig. 9), and Shafter 1975 (Fig. 10). Discrepancies in the magnitudes of flights (i.e., on a log scale) occurred in all three tests, but this was expected. The important point is that the patterns of moth flights are followed reasonably well by the model.

Results for Firebaugh 1974 (Fig. 11), the last location in the San Joaquin Valley, were not as satisfactory as those just described. The model did not predict the peak flight of early September, but did mimic the observed pattern fairly well from mid-September

TABLE 6.

A COMPARISON OF DAY DEGREE ACCUMULATIONS, CROPPING PATTERNS, AND LOCATION AND EXPOSURE OF THE LIGHT TRAPS AT THE FIVE STUDY SITES (1974)

| Location	ΣD° >12.2 °C	Major potential BAW hosts	Trap location	Trap exposure
San Joaquin Valley				
Firebaugh	2,407	cotton, alfalfa, sugar beets		270°
Corcoran	2,392	cotton, alfalfa	Edge of cotton field	360°
Shafter	2,501	cotton, alfalfa		180°
Sacramento Valley				
Davis	2,024	alfalfa, sugar beets	Near campus buildings	180°
Salinas Valley				
Gonzales	1,364	alfalfa, many vegetable crops	Edge of alfalfa field	180°
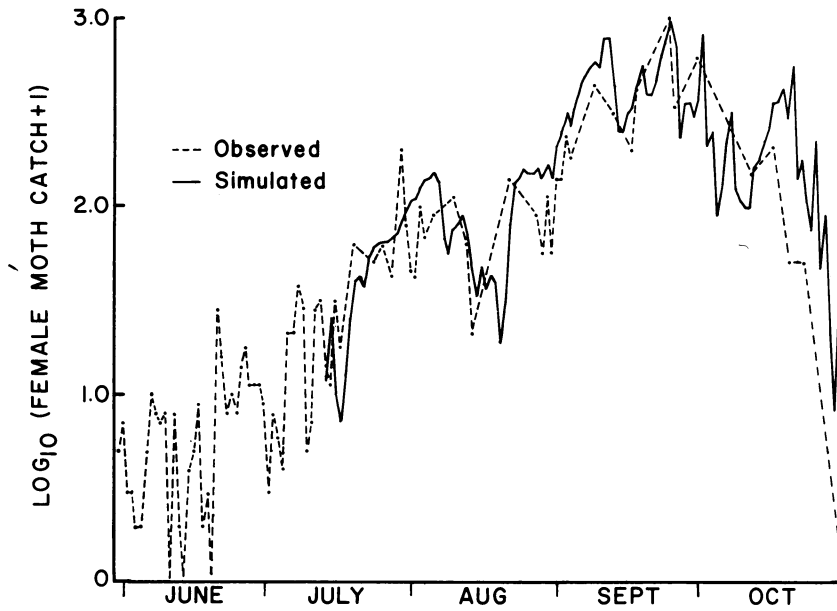
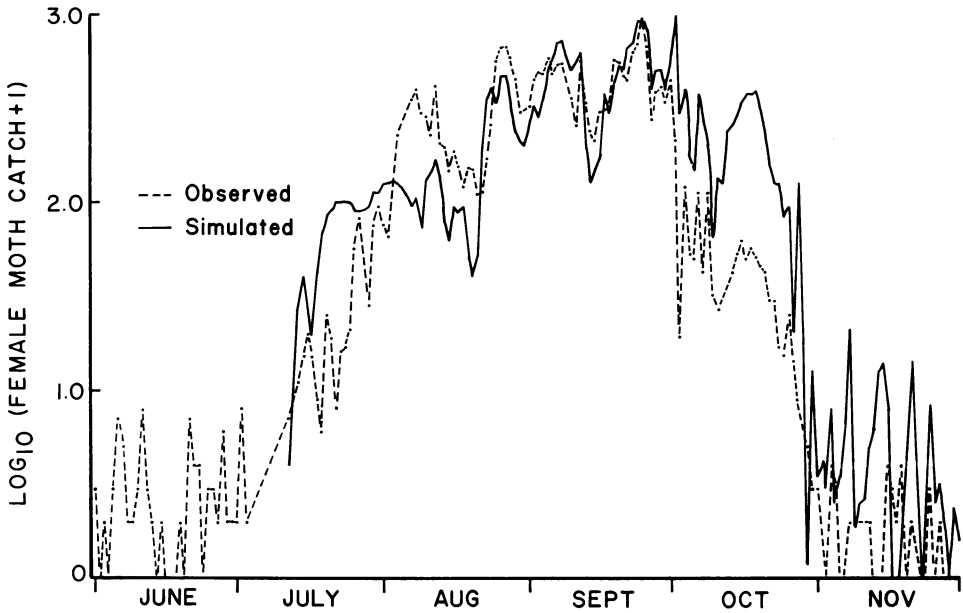Fig. 8. Observed and simulated light trap catches of female beet armyworms, Corcoran 1974.

Fig. 9. Observed and simulated light trap catches of female beet armyworms, Shafter 1974.
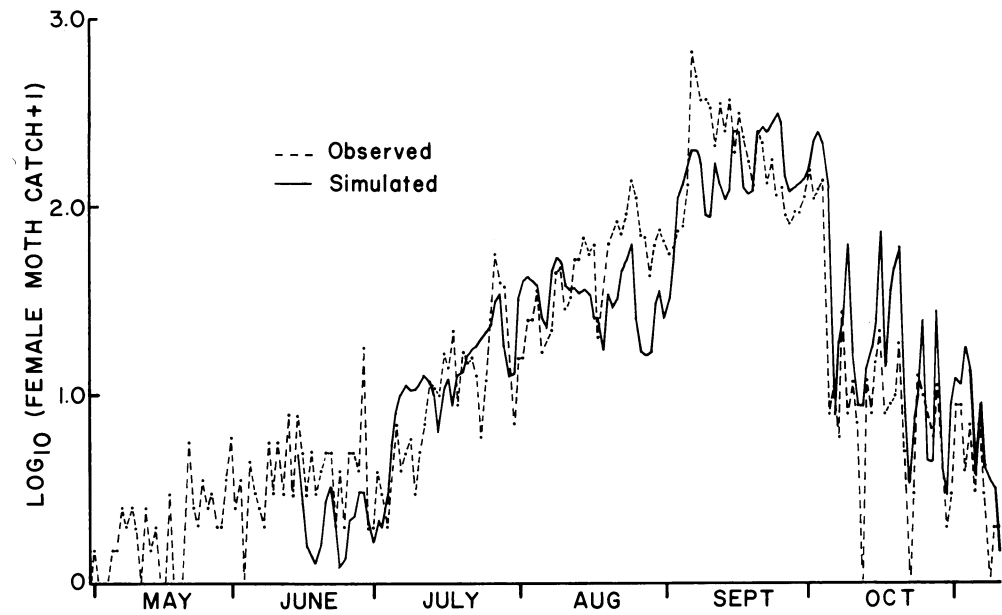
Fig. 10. Observed and simulated light trap catches of female beet armyworms, Shafter 1975.
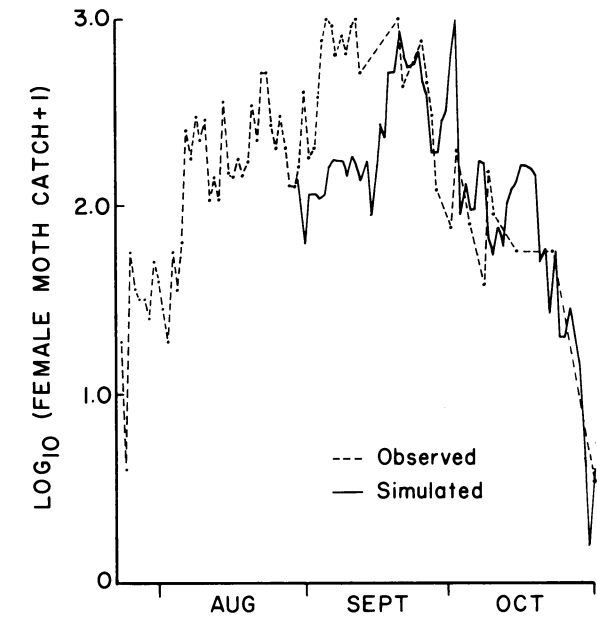

Fig. 11. Observed and simulated light trap catches of female beet armyworms, Firebaugh 1974.

TABLE 7.

INCLUSIVE DATES OF LIGHT TRAP DATA USED FOR INITIALIZING EACH SIMULATION

Site	Year	Dates
Corcoran	1974	5/28 to 7/7
Shafter	1974	5/31 to 7/10
Shafter	1975	4/29 to 6/13
Firebaugh	1974	7/24 to 8/27
Davis	1974	7/5 to 8/9
Gonzales	1974	7/7 to 9/21

to late October. This simulation was initialized with data from much later in the summer than the other three (Table 7), because earlier samples were not adequately preserved and many moths were unidentifiable. Initializing with light trap data from this period, particularly considering that well over one hundred moths were collected on many nights, may have resulted in errors in estimating the size and age structure of the adult population.

Results of the simulation conducted for the location in the Sacramento Valley (Davis, 1974; Fig. 12) indicate a good fit of the model's predictions with the observed data. This test was initialized with data beginning in early July (Table 7). Although the light trap was operated at Davis beginning in late May, very few BAW moths were caught before July.

Results of the simulation conducted for the location in the Salinas Valley (Gonzales, 1974, Fig. 13) indicate that the model was not able to match the observed data. Initialization data for this test needed to be supplied for approximately ten weeks (Table 7) due to cool summer temperatures which resulted in extended developmental times (in days) for the immature stages.

Analysis and criticism of the model. In general, the model was able to mimic the patterns of BAW moth flights for locations within the Great Central Valley (San Joaquin and Sacramento valleys), which indicates that a good understanding of the processes which determine BAW flight phenology in this region has been incorporated. Why the model failed to predict the observed patterns in the Salinas Valley would require further investigation, though it is likely related to the summer climate of this region, which is cool with frequent strong winds and fog. However, its failure provides useful knowledge of the limits to the range of conditions in which the model furnishes a valid description.

Since the model is driven by temperature, its apparent validity under conditions in the Central Valley suggests that temperature is of prime importance in producing the observed patterns of BAW flights. In the model, temperature produces the predicted pattern through two main influences: 1) it determines the rate at which individuals in the population age and reproduce, which directly affects the rate at which the population grows (or declines); and 2) it determines the activity levels of the adults, which directly affect the sampling efficiency of the light trap.

The relative contributions of these two influences would be difficult to experimentally determine in the field, but they can be easily separated with the model. Figure 14 shows the results of the simulation for Corcoran (1974) with the activity scalar removed from the model, i.e., the simulated light trap catch equals the number of ovipositing females.

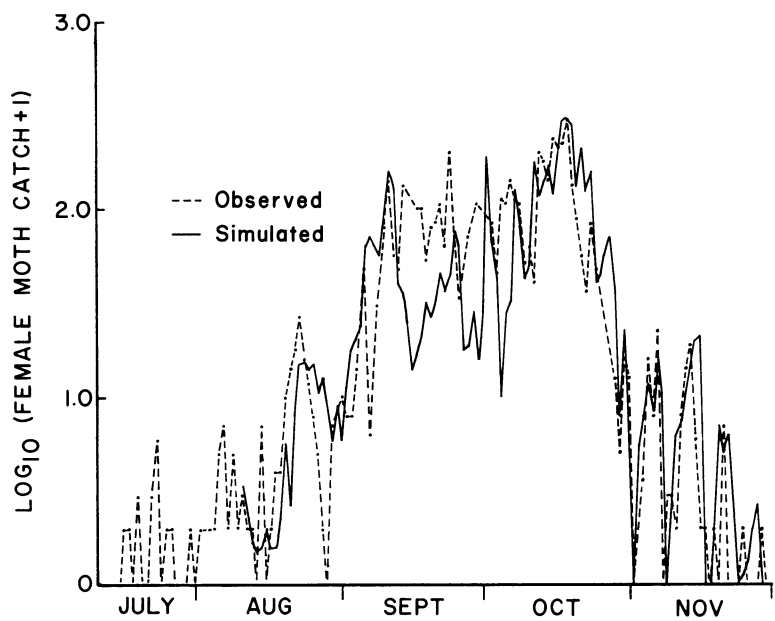Fig. 12. Observed and simulated light trap catches of female beet armyworms, Davis 1974.
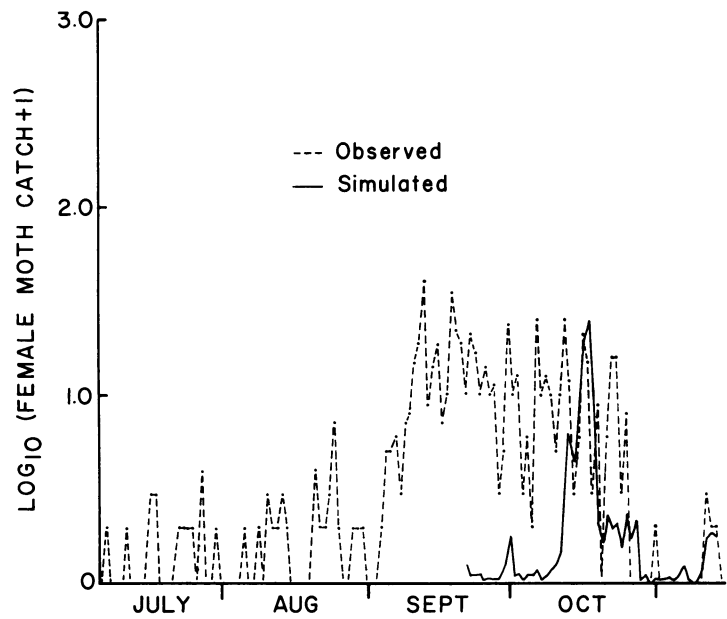

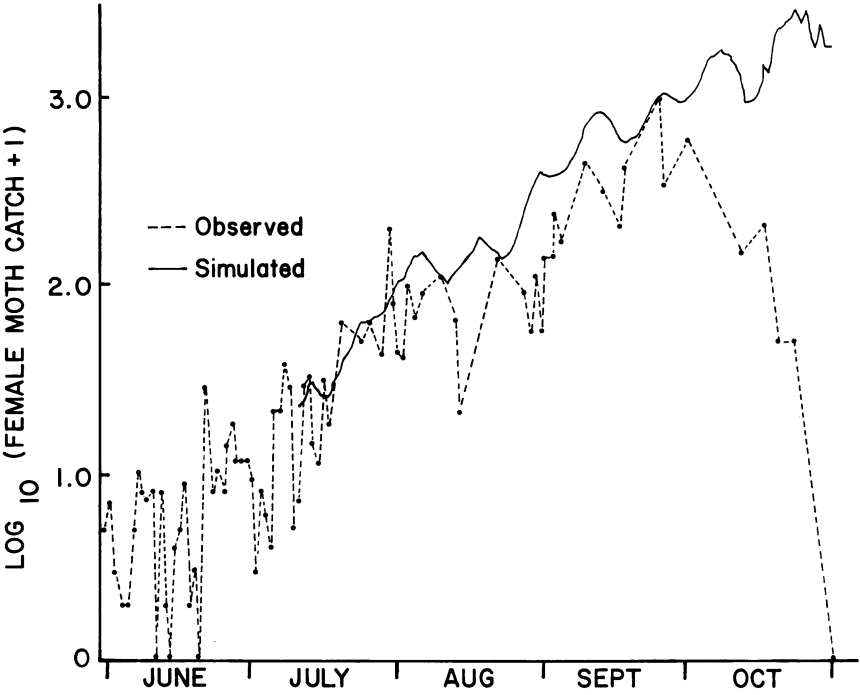Fig. 13. Observed and simulated light trap catches of female beet armyworms, Gonzales 1974.

Fig. 14. Observed light trap catches of female beet armyworms and simulated populations of ovipositing beet armyworms, Corcoran 1974.
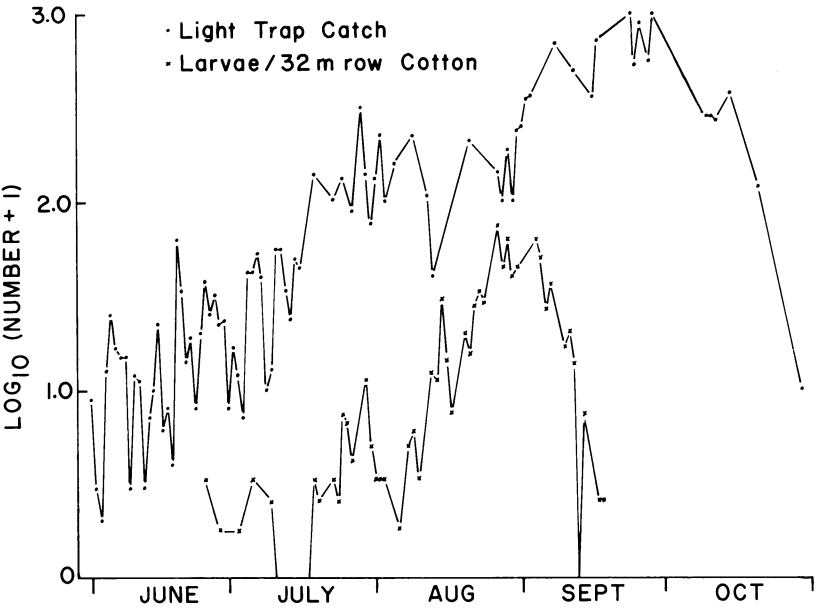

Fig. 15. Beet armyworm larval populations in cotton and light trap catches, Corcoran 1974.

The model still reproduced the general pattern of buildup to the peak flight, but it failed to mimic the subsequent decline in trap catch (cf. Fig. 8). This behavior was found for all locations; in general, the predicted late season declines in trap catch are due to the influence of the activity scalar. This suggests that the suppression of flight activity by cool temperatures is responsible for the late season declines in the field.

However, there are factors other than temperature which could limit BAW population growth during the late season period. One of these, host availability, is illustrated by a comparison of BAW larval counts in cotton (unpublished data of A. P. Gutierrez and D. Westphal) and light trap catches, again at Corcoran during 1974 (Fig. 15). Larval numbers declined sharply during September primarily because the plants were senescing. The lag time from the peak in larval numbers (late August and early September) to the peak in adult numbers (late September) is about 300 D ° $>$ 12.2 °C, which equals the time required for pupal development plus about one half the time for larval development. Cotton is easily the most abundant host available to the BAW in the Corcoran area, hence these data indicate that host availability (senescence), a factor not included in the model, may be ultimately responsible for the late season decline in moth flights.

Data are not available concerning mechanisms which limit BAW population growth in other areas. For example, a major host of the BAW in the Sacramento Valley is alfalfa, so field populations would not appear to be influenced to such a great extent by late season availability of this host, though there may be other factors, such as disease epizootics, operating. Thus, although the model is deficient to the extent that it does not incorporate factors which may be ultimately limiting, this deficiency is masked by its understanding of the proximate mechanism which produces the observed late season patterns of light trap catches.

CONCLUSION

New insights into the functioning of BAW populations have been gained through our modeling effort. We were able to isolate and examine the relationship between weather and the timing and patterns of BAW moth flights, and we demonstrated that temperature plays a major role in determining BAW flight phenology. Although the model does not include all factors which influence the dynamics of BAW populations, it does provide a realistic ecological framework for the incorporation of these factors.

Models of the kind developed in this study can also be extended for use in pest management programs to 1) develop models of single pest-crop interactions (e.g., Gutierrez, Butler *et al.*, 1977; Gutierrez, Leigh *et al.*, 1977; Gutierrez, Christensen *et al.*, 1976); 2) develop multiple species ecosystem models; 3) provide short-term prediction in an on-line system (e.g., Giese, Peart, and Huber, 1975); or 4) aid in the formulation of optimization models for crop protection (e.g., Regev, Gutierrez and Feder, 1976; Shoemaker, 1976).

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APPENDIX A

This appendix presents the results of investigations into the relationships between BAW total fecundity and adult size, temperature, and larval host. The analyses were conducted to obtain an estimate of total fecundity to use in the phenology model.

The first hypothesis tested was that total fecundity varies with the size of the female, with larger females laying a greater number of eggs. The character used for an index of adult size was the length of the metathoracic femur, since this length was found to vary isometrically with female pupal weight (Fig. 1A). Regression analysis was used to determine the relationship between fecundity (dependent variable) and size (independent variable) for data obtained from different combinations of experimental conditions (Table 1A). Although in actuality size is not fixed, but is a random variable, the use of regression analysis is valid (Neter and Wasserman, 1974, p.76). Tests of regression indicated ($a = .05$) a significant positive relationship between total fecundity and size for each combination of temperature and host (Table 1A). A similar relationship, but between fecundity and female pupal weight, has been reported for *Trichoplusia ni* (Shorey, 1963).

Fig. 1A. Correlation between pupal weight and size of female beet armyworm moths reared in the laboratory.

The relationship between temperature and total fecundity was analyzed for the moths reared from artificial diet. The equations of fecundity as a function of size (Table 1A, host = diet) were used to adjust total fecundity to a size of 2.7 mm (the mean size of females used in these experiments) in a manner described by equations 1A and 2A.

$$\phi_{2.7} = f_{2.7} + d_i$$

$$d_i = \phi_i - f_i$$

where

$\phi_{2.7}$ = adjusted fecundity for mean size (2.7 mm).

$f_{2.7}$ = predicted fecundity for mean size (2.7 mm).

d_i = deviation of observed from predicted fecundity at observed size.

ϕ_i = observed fecundity.

f_i = predicted fecundity at observed size.

TABLE 1A.

RESULTS OF REGRESSION ANALYSES OF FECUNDITY ON ADULT SIZE FOR BEET ARMYWORMS
AT DIFFERENT CONSTANT TEMPERATURES AND REARED FROM DIFFERENT HOSTS

Temperature (°C)	Host	Estimates of parameters $\hat{b}$	$\hat{a}$	r^2	N	T*
15.6	Diet	1,072	− 1,911	.40	10	2.337 (p = .024)
21.1	Diet	1,659	− 3,337	.78	16	7.094 (p ∙< .001)
21.1	Alfalfa	880	− 1,516	.69	14	5.310 (p < .001)
21.1	Cotton	759	− 1,270	.60	9	3.096 (p = .009)
26.7	Diet	1,790	− 3,469	.87	14	9.033 (p < .001)

* Test of $H_0 : b = 0$ vs. $H_1: b \neq 0$.

Substantial reduction in variability was gained by standardizing fecundity for size, though the means are influenced little (Table 2A). The results of an analysis of variance performed on the adjusted data strongly suggest (p < .001) that BAW fecundity was influenced by the temperatures used. To test the hypothesis that fecundity increased with increasing temperature, pairwise comparisons were made using Bonferroni's inequality (Neter and Wasserman, 1974). This procedure retains a chosen error rate for the entire analysis by partitioning the error equally over all comparisons. Using an overall error rate of .05 with three one-sided comparisons, the error rate for each comparison is .05/3 or .0167 (i.e., for any comparison to show significance, the probability of obtaining a t-value as large or larger than the one observed must be less than .0167). The results of this analysis (Table 3A) indicate, for the mean size and three temperatures used, a positive relationship between temperature and total fecundity.

The relationship between larval host and total fecundity was analyzed for the experiments conducted at 21.1 °C, using the equations of fecundity as a function of size (Table 1A, temperature = 21.1°). Covariance analysis, utilizing the generalized F-ratio, was used to test if the slopes (b) of the three equations differed. The essence of the generalized F-ratio is to establish two or more nested hypotheses, from least to most restrictive, and use the F distribution to test whether the increase in the residual mean square

TABLE 2A.

OBSERVED AND ADJUSTED (FOR SIZE) BEET ARMYWORM FECUNDITY AT CONSTANT
TEMPERATURES (MOTHS WERE REARED FROM ARTIFICIAL DIET)

Temperature (°C)	N	Observed Mean	S.D.	Adjusted Mean	S.D.
15.6	10	948.4	257.4	983.9	198.4
21.1	16	1,199.4	322.3	1,141.1	150.5
26.7	14	1,285.4	374.7	1,364.3	136.8

TABLE 3A.

RESULTS OF PAIRWISE COMPARISONS, USING BONFERRONI'S INEQUALITY
(ONE TAILED TESTS), FOR THE INFLUENCE OF TEMPERATURE ON BEET ARMYWORM
FECUNDITY ADJUSTED FOR SIZE ($\bar{x}_1 = 15.6°, \bar{x}_2 = 21.1°, \bar{x}_3 = 26.7°C$)

Comparison	$\lvert \bar{x}_i - \bar{x}_{i'} \rvert$	$S_P\sqrt{\dfrac{1}{n_i} + \dfrac{1}{n_{i'}}}$	T*
$\bar{x}_1$ vs. $\bar{x}_2$	156.0	62.4	2.5018 (p = .009)
$\bar{x}_1$ vs. $\bar{x}_3$	380.4	64.1	5.9381 (p < .001)
$\bar{x}_2$ vs. $\bar{x}_3$	224.3	56.6	3.9623 (p < .001)

* $T = \lvert \bar{x}_i - \bar{x}_{i'} \rvert / (S_P\sqrt{\dfrac{1}{n_i} + \dfrac{1}{n_{i'}}})$

which results from adopting a more restrictive hypothesis is sufficiently large to reject that hypothesis. The details of this procedure are given by Brand *et al.,* (1975).

The estimates of the regression parameters under the hypotheses that (1) the slopes are different (H_1), and (2) the data can be adequately described by a pooled slope (H_2), are given in Table 4A. The results of the covariance analysis (Table 4A) suggest that differences in the slopes exist. Bonferroni's inequality was used to test which slopes differed. Using an overall error rate of .05 with three two-sided comparisons, the error rate for each comparison is .05/6 or .0083. The results of this analysis (Table 5A) suggest that the slopes of the equations for cotton and alfalfa are not different, but that both differ from the slope of the equation for artificial diet.

The data therefore support the conclusion that an estimate of the slope pooled from the cotton and alfalfa regressions adequately describes both. Covariance analysis was used to test if the intercepts of the cotton and alfalfa regression equations differed. Estimates of the regression parameters under the hypotheses that (1) the slopes are equal, but the intercepts are different (H_2), and (2) both slopes and intercepts are equal (H_3), are given in Table 6A. The results of the covariance analysis (Table 6A) suggest that the intercepts are not different, i.e., that all the individuals were drawn from the same population.

TABLE 4A.

RESULTS OF THE COVARIANCE ANALYSIS OF THE HOMOGENEITY OF SLOPES FOR BEET ARMYWORM
FECUNDITY-ON-SIZE REGRESSIONS AT 21.1°C AS INFLUENCED BY LARVAL HOST.

Model	Larval host	Estimates of parameters $\hat{a}$	Estimates of parameters $\hat{b}$	Degrees of freedom	Residual sum of squares	F*
$H_1 : E(Y_{ij}/X_{ij}) = a_i + b_iX_{ij}$	Cotton	759	−1270	$n_1 = 33$	$SS_1 = 554{,}827$	5.503 (p = .009)
	Alfalfa	880	−1516			
	Artificial diet	1659	−3337			
$H_2 : E(Y_{ij}/X_{ij}) = a_{wi} + b_wX_{ij}$	Cotton	1172	−2308	$n_2 = 35$	$SS_2 = 739{,}867$	
	Alfalfa	1172	−2201			
	Artificial diet	1172	−2008			

*$F = [(SS_2 - SS_1)/(n_2 - n_1)]/[SS_1/n_1]$ has the F distribution with $n_2 - n_1$ and n_1 degrees of freedom.

TABLE 5A.

RESULTS OF PAIRWISE COMPARISONS, USING BONFERRONI'S INEQUALITY, OF SLOPES FOR
BEET ARMYWORM FECUNDITY-SIZE REGRESSIONS AT 21.1°C AS INFLUENCED BY
LARVAL HOST ($\hat{b}_1$ = COTTON, $\hat{b}_2$ = ALFALFA, $\hat{b}_3$ = ARTIFICIAL DIET).

Comparison	$\hat{b}_i - \hat{b}_{i'}$	$S\hat{b}_i - \hat{b}_{i'}$	T^*
$\hat{b}_1$ vs. $\hat{b}_2$	120.5298	333.4936	0.3614 (p = .36)
$\hat{b}_1$ vs. $\hat{b}_3$	898.6882	324.6567	2.7681 (p = .005)
$\hat{b}_2$ vs. $\hat{b}_3$	778.1584	285.8053	2.7227 (p = .005)

$^*T = |\hat{b}_i - \hat{b}_{i'}| / S\hat{b}_i - \hat{b}_{i'}$

TABLE 6A.

RESULTS OF THE COVARIANCE ANALYSIS OF THE HOMOGENEITY OF INTERCEPTS FOR BEET ARMYWORM
FECUNDITY-ON-SIZE REGRESSIONS AT 21.1°C AS INFLUENCED BY LARVAL HOST (COTTON AND ALFALFA ONLY)

Model	Larval host	Estimates of parameters $\hat{b}$	$\hat{a}$	Degrees of freedom	Residual sum of squares	F^*
$H_2 : E(Y_{ij}/X_{ij}) = a_{wi} + b_w X_{ij}$	Cotton	833	-1454	$n_2 = 20$	$SS_2 = 222,807$	0.896 (p = .36)
	Alfalfa	833	-1406			
$H_3 : E(Y_{ij}/X_{ij}) = a_t + b_t X_{ij}$	Cotton	776	-1288	$n_3 = 21$	$SS_3 = 232,784$	
	Alfalfa	776	-1288			

$^* F = [(SS_3 - SS_2)/(n_3 - n_2)]/[SS_2/n_2]$ has the F distribution with $n_3 - n_2$ and n_2 degrees of freedom.

TABLE 7A.

SIZES (METATHORACIC FEMUR LENGTHS) OF FEMALE BEET ARMYWORM MOTHS.
SHAFTER, 1976

Date(s) collected	N	Mean size (mm)	S.D.
5/12–26	25	2.90	.1411
6/27	25	2.84	.1725
7/26	25	2.80	.1466
8/24	25	2.75	.1140
9/20	25	2.80	.1123
10/14	25	2.81	.1347
Total	150	2.82	.1439

Two major hosts of the BAW in the San Joaquin Valley are cotton and alfalfa, hence this pooled equation of fecundity as a function of size was used to obtain an estimate of total fecundity for field moths. The average sizes of females taken at Shafter during 1976 are given in Table 7A. Substituting the overall mean size of field females (2.82 mm) in the equation produces a value of approximately 900 eggs for total fecundity, and this is the estimate used for the model.

APPENDIX B

The Beet Armyworm Algorithm

```
      PROGRAM BAWSIM (INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
C  THIS IS A MODEL OF THE FLIGHT PHENOLOGY OF THE BEET ARMYWORM.  THE
C  ALGORITHM OPERATES IN DEGREES FAHRENHEIT.  DATA REQUIRED ARE THE
C  DAILY MAX AND MIN TEMPERATURES, ENTERED AS DATA STATEMENTS IN ITEMP
C  (BEGIN WITH MIN), AND AN INITIAL MOTH POPULATION, ENTERED AS DATA
C  STATEMENTS IN ADNUM.  ALL OTHER ARRAYS ARE INITIALIZED WITH ZEROS
C  (INCLUDING THE REMAINING ELEMENTS OF ADNUM).  ALSO, THE FIRST AND
C  LAST DAYS (FDAY AND LDAY) AND TOTAL IMMATURE MORTALITY (XMORT) MUST
C  BE SPECIFIED.
      COMMON/AGES/AGE1,AGE2,AGE3,BAWAGE(365)
      COMMON/CATCH/CATCH1,CATCH2,CATCH3,CATCH4
      COMMON/COUNT1/INEW,IOLD
      COMMON/COUNT2/LNEW,LOLD
      COMMON/DATE/MONTH,DAY
      COMMON/DAY/IDAY
      COMMON/DDEG1/DDIMM
      COMMON/DDEG2/DDADLT
      COMMON/DDEG3/DD50,DD54,DDNITE,SUM1
      COMMON/MORT/R,ESURV
      COMMON/MTHAGE/ADAGE(365)
      COMMON/NUMBER/ADNUM(364),BAWNUM(365)
      COMMON/NUMBRS/PUPAE,WORMS,EGGOLD,EGGNEW,PREOV,OVIPAD
```

```
      COMMON/OVRATE/A1,B1,A3,B3,FEC
      COMMON/SCALE/ASCALE,BSCALE
      COMMON/TEMPS/T50,T54,T60,T90,ITEMP(730)
      INTEGER FDAY
C*********************************************************************
C  SPECIFY FIRST (FDAY) AND LAST (LDAY) DAY FOR THIS SIMULATION,EGG
C  (EMORT) AND TOTAL (XMORT) IMMATURE MORTALITIES, DEVELOPMENTAL TIMES
C  FOR IMMATURE STAGES (AGE1,AGE2,AGE3), AND FECUNDITY(FEC)
      FDAY=176
      LDAY=260
      XMORT=99.2
      EMORT=39.35
      AGE1=94.0
      AGE2= 564.0
      AGE3=882.0
      FEC=900.0
C*********************************************************************
  132 FORMAT (10X,*BAW SIMULATION - LOCATION AND DATE*/,
     *10X,
     **EGG MORTALITY=*,F5.2/,10X,*LARVAL MORTALITY=*F5.2/,
     *10X,*TOTAL IMMATURE MORTALITY=*,F5.2///)
      IOLD=FDAY-2
      LOLD=FDAY-2
      MONTH=1
      ASCALE=1.465140574
      BSCALE=0.4590422844
      SUM1=0.0
      A1=2.326484605
      B1=-0.1315461847
      A3=1.473399699
      B3=-0.0223379845
      T50=50.0
      T54=54.0
      T60=60.0
      T90=90.0
C  INITIALIZE AGE AND NUMBER ARRAYS TO ZERO
      DO 1 I=IOLD,LDAY
       BAWAGE(I)=0.0
       ADAGE(I)=0.0
       BAWNUM(I)=0.0
    1 CONTINUE
C  CALCULATE VALUES OF ESURV AND R FOR SPECIFIED MORTALITES
      ESURV=-(EMORT/100.0)/AGE1
      X1=(1.0-(XMORT/100.0)/(1.0-(EMORT/100.0)
      CMORT=(1.0-X1)*100.0
      R-ALOG(X1)/(AGE2-AGE1)
      PRINT 132,EMORT,CMORT,XMORT
       DO 10 IDAY=FDAY,LDAY
        CALL TMPSUM
        CALL DEVEL
        CALL EGGLAY
        CALL MODAYS
        CALL CALC
        PRINT 133,MONTH,NDAY,DDIMM,SUMI,DDADLT,DDNITE,EGGNEW,EGGOLD,
     *  WORMS,PUPAE,PREOV,OVIPAD,CATCH3,CATCH4,CATCH1,CATCH2
   10  CONTINUE
  133 FORMAT(5X,I2,*/*,I2,2X,*DD IMMATURES=*,F5.2,2X
     **SUM DD IMMATURES=*,F8.2,2X,*DD ADULTS=*F5.22X,
     **NIGHT DD=*,F5.2/,10X,*NEW EGGS=*,F11.2,2X,*OLD EGGS=*,
```

```
      *F11.2,2X,*LARVAE=*,F11.2,2X,*PUPAE=*,F11.2/,10X,
      **PREOV FEMALES=*,F11.2,2X,*OVIP FEMALES=*F11.2,2X,
      **OPTIMUM FEMALE CATCH=*,F9.2,2X,*LOG 10 (CATCH + 1)=*,
      *F5.2/,64X*SCALED FEMALE CATCH=*,F9.2,2X,
      **LOG 10 (CATCH + 1)=*,F5.2//)
       STOP
       END



       SUBROUTINE TMPSUM
C
C************************************************************************
C  THIS SUBROUTINE CALCULATES DAY DEGREES TWICE,DAILY, BY
C  INTEGRATING A SIN FUNCTION FIT THROUGH TODAY'S MIN AND MAX (FIRST
C  HALF) AND TODAY'S MAX AND TOMORROW'S MIN (SECOND HALF).  THIS IS
C  DONE FOR SPECIFIED THRESHOLDS.  THE CALCULATIONS ARE TAKEN FROM
C  TEMPSUM, WRITTEN BY N. GILBERT.
C************************************************************************
C
       COMMON/DAY/IDAY
       COMMON/DDEG1/DDIMM
       COMMON/DDEG2/DDADLT
       COMMON/DDEG3/DD50,DD54,DDNITE,SUM1
       COMMON/TEMPS/T50,T54,T60,T90,ITEMP(730)
       DDIMM=0.0
       DDADLT=0.0
       J=2*IDAY-1
       XMIN=FLOAT(ITEMP(J))
       J=J+1
       XMAX=FLOAT(ITEMP(J))
    60 CONTINUE
C  CALCULATE DAY DEGREES FOR T=50
       Y=XMAX+XMIN-2.0*T50
       IF (XMIN .LT. T50) GO TO 42
       DD50=0.25*Y
       GO TO 41
C  IF MIN GT 50, GO TO DD CALC. FOR T=54
    42 CONTINUE
       IF (XMAX .GT. T50) GO TO 43
       DD50=0.0
       DD54=0.0
       GO TO 50
C  IF MAX LT 50, TERMINATE ALL DD CALCS.
    43 CONTINUE
       SINE=Y/(XMIN-XMAX)
       T=ASIN(SINE)
       C+0.079577472*((XMAX-XMIN)*COS(T)-Y*T)
       DD50=C+0.125*Y
C  CALCULATE DAY DEGREES FOR T=54
    41 CONTINUE
       Y=XMAX+XMIN-2.0*T54
       IF (XMIN .LT. T54) GO TO 52
       DD54=0.25*Y
       GO TO 50
C  IF MIN GT 54, GO TO DD CALCS. FOR T=60 AND 90
    52 CONTINUE
       IF (XMAX .GT. T54) GO TO 53
       DD54=0.0
       GO TO 50
```

```
   53 CONTINUE
      SINE=Y/(XMIN-XMAX)
      T=ASIN(SINE)
      C=0.079577472*((XMAX-XMIN)*COS(T)-Y*T)
      DD54=C+0.125*Y
   50 CONTINUE
      DDIMM=DDIMM+DD54
      DDADLT=DDADLT+DD50
C  CHECK TO SEE IF THIS IS THE FIRST OR SECOND RUN FOR THE DAY
      TEMP=FLOAT(ITEMP(J))
      IF (XMIN .EQ. TEMP) GO TO 40
      J=J+1
      XMIN+FLOAT(ITEMP(J))
      GO TO 60
   40 CONTINUE
C  CALCULATE DAY DEGREES FOR T=60
      IF (XMAX .GT. T60) GO TO 61
      DD60=0.0
      DD90=0.0
      GO TO 62
C  IF MAX LT 60, SKIP DD CLACS. FOR T=60 AND 90
   61 CONTINUE
      X=YMAX+XMIN-2.0*T60
      IF (XMIN .LT. T60) GO TO 63
      DD60=0.25*Y
      GO TO 64
C  IF MIN GT 60, GO TO DD CALCS. FOR T=90
   63 CONTINUE
      SINE=Y/(XMIN-XMAX)
      T=ASIN(SINE)
      C=0.079577472*((XMAX-XMIN)*COS(T)-Y*T)
      DD60=C+0.125*Y
C  CALCULATE DAY DEGREES FOR T=90
   64 CONTINUE
      IF (XMAX .GT. T90) GO TO 65
      DD90=0.0
      GO TO 62
C  IF MAX LT 90, SKIP DD CALCS. FOR T=90
   65 CONTINUE
      Y=XMAX+XMIN-2.0*T90
      SINE=Y/(XMIN-XMAX)
      T=ASIN(SINE)
      C=0.079577472*((XMAX-XMIN)*COS(T)-Y*T)
      DD90=C+0.125*Y
   62 CONTINUE
      DDNITE=DD60-DD90
      SUM1=SUM1+DDIMM
      RETURN
      END



      SUBROUTINE DEVEL
C
C**********************************************************************
C  THIS SUBROUTINE INCREMENTS THE AGES AND DETERMINES SUVIVORSHIP FOR
C  ALL CCHORTS OF BAW IMMATURES.
C**********************************************************************
C
      COMMON/AGES/AGE1,AGE2,AGE3,BAWAGE(365)
```

```
      COMMON/COUNT1/INEW,IOLD
      COMMON/DAY/IDAY
      COMMON/DDEG1/DDIMM
      COMMON/MORT/R,ESURV
      COMMON/NUMBER/ADNUM(365),BAWNUM(365)
      REAL LXLAR1,LXLAR2,LXEGG1,LXEGG2
      INEW=IDAY-1
      IDROP=0
      DO 20 I=IOLD,INEW
        IF (BAWAGE(I) .LT. AGE2) GO TO 21
C  DETERMINE PUPAL DEVELOPMENT
        BAWAGE(I)=BAWAGE(I)+DDIMM
        IF (BAWAGE(I) .LT. AGE3) GO TO 20
C  DETERMINE MOTH EMERGENCE
        ADNUM(IDAY)=ADNUM(IDAY)+BAWNUM(I)
        IDROP=IDROP+1
        GO TO 20
   21 CONTINUE
      IF(BAWAGE(I) .LT. AGE1) GO TO 42
C  DETERMINE LARVAL DEVELOPMENT AND SURVIVORSHIP
      LXLAR1=EXP(R*(BAWAGE(I)-AGE1))
      BAWAGE(I)=BAWAGE(I)+DDIMM
      CATAGE=BAWAGE(I)
      IF (BAWAGE(I) .GT. AGE2) CATAGE+AGE2
      LXLAR2=EXP(R*(CATAGE-AGE1)
      BAWNUM(I)=(LXLAR2/LXLAR1)*BAWNUM(I)
      GO TO 20
C  DETERMINE EGG DEVELOPMENT AND SURVIVORSHIP
   22 CONTINUE
      LXEGG1=1.0-ESURV*BAWAGE(I)
      BAWAGE(I)=BAWAGE(I)+DDIMM
      EGGAGE=BAWAGE(I)
      IF (BAWAGE(I) .GT. AGE1) EGGAGE=AGE1
      LXEGG2=1.0-ESURV*EGGAGE
      BAWNUM(I)=(LXEGG2/LXEGG1)*BAWNUM(I)
      IF (BAWAGE(I) .LE. AGE1) GO TO 20
      LXLAR2=EXP(R*(BAWAGE(I)-AGE1))
      BAWNUM(I)=LXLAR2*BAWNUM(I)
   20 CONTINUE
      IOLD=IOLD+IDROP
      RETURN
      END


      SUBROUTINE EGGLAY
C
C**********************************************************************
C  THIS SUBROUTINE INCREMENTS THE AGES AND DETERMINES SURVIVORSHIP FOR
C  ALL CCHORTS OF BAW ADULTS, AND DETERMINES THE NUMBER OF EGGS LAID.
C**********************************************************************
C
      COMMON/COUNT2/LNEW,LOLD
      COMMON/DAY/IDAY
      COMMON/DDEG2/DDADLT
      COMMON/MTHAGE/ADAGE(365)
      COMMON/NUMBER/ADNUM(365),BAWNUM(365)
      COMMON/OVRATE/A1,B1,A3,B3,FEC
      REAL NEWEGG,LXMTH1,LXMTH2
      LNEW=IDAY-2
```

```
      LDROP=0
      DO 30 I=LOLD,LNEW
       IF (ADAGE(I) .GT. 0.0) GO TO 31
       PER1=0.0
       GO TO 32
   31  CONTINUE
       PER1=1.0-A3*EXP(B3*ADAGE(I))
       IF (PER1 .LT. 0.0) PER1=0.0
   32  CONTINUE
       ADAGE(I)=ADAGE(I)+DDADLT
       IF (ADAGE(I) .EQ. 0.0) GO TO 33
       PER2=1.0-A3*EXP(B3*ADAGE(I))
       IF (PER2 .LT. 0.0) PER2=0.0
       NEWEGG=((PER2-PER1)*FEC)*(ADNUM(I)/2.0)
       BAWNUM(IDAY)=BAWNUM(IDAY)+NEWEGG
       IF (PER2 .GT. 0.99) GO TO 34
   33  CONTINUE
       XLONG=FLOAT(IDAY-I+1)
       IF (XLONG .LT. 11.0) GO TO 30
       LXMTH1=A1+B1*(XLONG-1.0)
       LXMTH2=A1+B1*XLONG
       IF (LXMTH2 .LE. 0.0) GO TO 34
       ADNUM(I)=(LXMTH2/LXMTH1)*ADNUM(I)
       GO TO 30
   34  CONTINUE
       LDROP=LDROP+1
   30 CONTINUE
      LOLD=LOLD+LDROP
      RETURN
      END




      SUBROUTINE MODAYS
C
C*********************************************************************
C  THIS SUBROUTINE CONVERTS MODEL IDAY INTO MONTH/DAY.  IT IS TAKEN
C  ESSENTIALLY UNCHANGED FROM TEMPSUM, WRITTEN BY N. GILBERT.
C*********************************************************************
C
      COMMON/DATE/MONTH,NDAY
      COMMON/DAY/IDAY
      GO TO (1,2,3,4,5,6,7,8,9,11,12,13),MONTH
    1 CONTINUE
      IF (IDAY .GT. 31) GO TO 2
      MONTH=1
      NDAY=IDAY
      GO TO 115
    2 CONTINUE
      IF (IDAY .GT. 59) GO TO 3
      MONTH=2
      NDAY=LDAY-31
      GO TO 115
    3 CONTINUE
      IF (IDAY .GT. 90) GO TO 4
      MONTH=3
      NDAY=IDAY-59
      GO TO 115
```

```
      4 CONTINUE
        IF (IDAY .GT. 120) GO TO 5
        MONTH=4
        NDAY=IDAY-90
        GO TO 115
      5 CONTINUE
        IF (IDAY .GT. 151) GO TO 6
        MONTH=5
        NDAY=IDAY-120
        GO TO 115
      6 CONTINUE
        IF (IDAY .GT. 181) GO TO 7
        MONTH=6
        NDAY=IDAY-151
        GO TO 115
      7 CONTINUE
        IF (IDAY .GT. 212) GO TO 8
        MONTH=7
        NDAY=IDAY-181
        GO TO 115
      8 CONTINUE
        IF (IDAY .GT. 243) GO TO 9
        MONTH=8
        NDAY=IDAY-212
        GO TO 115
      9 CONTINUE
        IF (IDAY .GT. 273) GO TO 11
        MONTH=9
        NDAY=IDAY-243
        GO TO 115
     11 CONTINUE
        IF (IDAY .GT. 304) GO TO 12
        MONTH=10
        NDAY=IDAY-273
        GO TO 115
     12 CONTINUE
        IF (IDAY .GT. 334) GO TO 13
        MONTH=11
        NDAY=IDAY-304
        GO TO 115
     13 CONTINUE
        MONTH=12
        NDAY=IDAY-334
    115 CONTINUE
        RETURN
        END



        SUBROUTINE CALC
C
C********************************************************************
C  THIS SUBROUTINE CALCULATES THE TOTAL NUMBERS OF ALL STAGES OF THE
C  BAW, PLUS SCALES LIGHT TRAP CATCH ACCORDING TO NIGHT TEMPERATURES.
C********************************************************************
C
        COMMON/AGES/AGE1,AGE2,AGE3,BAWAGE(365)
        COMMON/CATCH/CATCH1,CATCH2,CATCH3,CATCH4
        COMMON/COUNT1/INEW,IOLD
        COMMON/COUNT2/LNEW,LOLD
```

```
      COMMON/DDEG3/DD50,DD54,DDNITE,SUM1
      COMMON/NUMBER/ADNUM(365),BAWNUM(365)
      COMMON/NUMBRS/PUPAE,WORMS,EGGOLD,EGGNEW,PREOV,OVIPAD
      COMMON/SCALE/ASCALE,BSCALE
        PUPAE=0.0
        WORMS=0.0
        EGGOLD=0.0
        EGGNEW=0.0
        PREOV=0.0
        OVIPAD=0.0
        DO 70 I=IOLD,INEW
         IF (BAWAGE(I) .LT. AGE2) GO TO 71
         PUPAE=PUPAE+BAWNUM(I)
         GO TO 70
   71    CONTINUE
         IF (BAWAGE(I) .LT. AGE1) GO TO 72
         WORMS=WORMS+BAWNUM(I)
         GO TO 70
   72    CONTINUE
         EGGOLD=EGGOLD+BAWNUM(I)
   70    CONTINUE
        K=INEW+1
        EGGNEW=BAWNUM(K)
C   DETERMINE HOW MANY MOTHS WILL BE CAUGHT
        DO 80 I=LOLD,LNEW
         OVIPAD=OVIPAD+(ADNUM(I)/2.0)
   80    CONTINUE
      ADLONG=FLOAT(LNEW-LOLD)+1.0
      SCALE1=(ASCALE*EXP(BSCALE*DDNITE)-1.0)/100.0
      IF (SCALE1 .GT. 1.0) SCALE1=1.0
      IF (SCALE1 .LT. 0.0) SCALE1=0.0
      CATCH1=SCALE1*(OVIPAD/ADLONG)
      CATCH2=ALOG10(CATCH1+1.0)
      CATCH3=OVIPAD/ADLONG
      CATCH4=ALOG10(CATCH3+1.0)
        KK=LNEW+1
        PREOV=ADNUM(KK)/2.0
        KK=KK+1
        PREOV=PREOV+(ADNUM(KK)/2.0)
      RETURN
      END
```

ACKNOWLEDGEMENTS