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16. Abstract

This report discusses the current state of knowledge dealing with the prediction of the overwintering population and spring emergence of Heliothis spp., a serious pest of numerous crops in the U.S. and the world. Current literature is reviewed in detail. Temperature and day length are the primary factors which program H. spp. larva for possible diapause. Although studies on the interaction of temperature and day length are reported in numerous papers, the complete diapause induction process has not been identified sufficiently to allow accurate prediction of diapause timing.

Mortality during diapause has been reported as highly variable. The factors causing mortality have been identified, but only a few have been quantified.

The spring emergence of overwintering H. spp. adults has been studied by a number of scientists. Sufficient data have been collected to allow the development of mathematical models which predict the timing of emergence. Timing predictions compare favorably to observed field data; however, prediction of actual numbers of emerging moths has not been possible.

The potential for use of spring emergence predictions in pest management applications, as an early warning of potential crop damage, are excellent. Research requirements to develop such an early warning system are discussed at the conclusion of the report.

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Predicting the Timing and Potential of the Spring Emergence of Overwintered Populations of Heliothis spp.

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INTRODUCTION

Heliothis spp. are among the most serious pests in Agriculture. These species have become critical pests of cotton, seriously limiting the profitability of this crop. In addition, other valuable crops such as corn, tomatoes, soybeans, grain sorghum, tobacco and many vegetables may be seriously damaged by infestations of H. spp.

In the western hemisphere there are two predominate H. spp., Heliothis zea (Boddie) (HZ) and Heliothis virescens (Fabricius) (HV). Sizeable populations of HZ, known commonly as corn earworm or cotton bollworm, typically appear in non-tropical areas by early summer and affects a wide variety of crops. The HV, with common name tobacco budworm, does not build to large numbers until late summer and has fewer known hosts.

In the eastern hemisphere two comparable species exist, Heliothis armigera (Hubner) (HA) and Heliothis punctigera Wallengren (HP). The "old world bollworm", HA, is closely related in its behavior to the HZ; while the HP is similar to HV in its biology.

Several population dynamics models have been developed for H. spp. (Hartstack and Witz 1980). These models, however, simulate only one season at a time and must be reinitialized to begin each new season. To be able to investigate management strategies over multiyear periods and provide more accurate and timely information to producers, models need to be developed which will simulate multiple years in continous fashion.

REVIEW OF LITERATURE

Overwintering Behavior:

H. spp. infest a field crop region seasonally in one of two ways -- from local overwintering or by migration. In the tropics and subtropics, H. spp. have continuous, year-around generations. In an area north of the tropics H. spp. overwinter by hibernating in a diapause state as pupae. The range of this area varies by species. HZ overwinter throughout most of the U.S. (Quaintance and Brues 1905, Snow and Copeland 1971) while the HV can survive only in the more southern states (Eger 1981).

Diapause is characterized by a physiologic change in which metabolism is greatly reduced, growth and development are retarded or stopped, body fat is increased, and water content is decreased. The combined effect provides the insect with a mechanism to survive adverse environmental conditions such as cold temperatures or drought (Adkisson et al. 1972).

Diapause is classified as either obligatory or facultative, based primarily on whether the insect is univoltine or multivoltine, respectively. In facultive species, such as H. spp., the diapause is determined by environmental conditions (Roach 1968, Ditman et al. 1940). An extensive review of the physiology and biochemistry of diapause in insects is presented by Lees (39, 53).

Initiation of Diapause:

Phillips and Newsom (1966) ran tests to determine the environmental factors which affected diapause in HZ and HV. They found the larval stage to be sensitive to photoperiod such that in 14 hrs of daylight larvae entering the pupal stage would not go into diapause, whereas larvae experiencing 10 hrs of daylight would go into diapause. Further, they determined that temperature also had an influence such that high temperatures would counteract the effect of short daylight periods and fewer HZ and HV would go into diapause. Low temperatures influenced the results at longer daylight periods, causing more pupae to enter diapause.

An additional finding of their research was a method for visually determining whether or not a pupa was in diapause. They reported that in diapause both HZ and HV retain larval eye spots in the postgenal region. This test has become a standard technique in diapause research.

Wellso (1966) and Wellso and Adkisson (1966) report a series of experiments dealing with the effect of temperature and photoperiod on HZ. They considered the effect of photoperiod not only on the larvae, but on the preceeding egg stage as well as the adult of the previous generation. They report that induction of diapause requires that the larval stage experience shorter daylight periods than the previous parent and egg stages. This would suggest a method for the insect to distinguish between fall and spring on photoperiod alone without the requirement of correlated, concurrent temperature effects. They also reported that induction of diapause in HZ only occurs in a limited time span with maximum induction occuring between mid October and mid November. The resulting function for percentage of the population initiating diapause over time was a bell shaped curve. In the experiment with photoperiod, no diapause was induced for daylight periods, including civil twilight, greater than than 13.33 hrs. Maximum induction occurred between 12 and 13 hrs. of daylight.

Roach (1968) also ran many experiments to study the effect of photoperiod and temperature on diapause induction. His results were similar to Wellso (1966). Maximum diapause occurred with decreasing temperatures below 16 C (air) and daylight decreasing to 11 hrs. He measured 98 to 100% diapause under these conditions. Eggs were hatched in 14 hour daylight in all cases. Results of laboratory experiments to simulate actual daylight periods were also similar to Wellso's results, with peak diapause occurring when daylight decreased to 11.5 hrs.

Adkisson et al. (1972) summarize the Texas research results for HZ. Maximum induction of diapause requires decreasing temperature, decreasing daylight period through the stages from parent to pupa, daylight period during the larval stage less than 13 hrs, and temperature of the larval stage going below 21 C. This results in a peak of 94% induction. Meola and Adkisson (1977) were able to repeat this result, obtaining 93% diapause with HZ under simultaneously decreasing daylight period and temperature.

Fye and Carranza (1973) studied diapause initiation in outdoor cages in Arizona using laboratory reared insects. They measured the percentage of pupae going into diapause weekly. Results were a bell shaped curve similar to that of Wellso (1966), but with timing shifted slightly. The timing shift would be expected due to the difference in latitude between the Arizona site and the location of Wellso's work in Texas.

Stinner et al. (1977) report data and regression results using a normal distribution to model percent induction into diapause. Their data, from North Carolina, vary from other data taken in Arizona, Texas, and Arkansas in two ways: (1) The model indicates percent diapause going to 100% for late season pupae, whereas other experimental data indicate it decreases back down to zero in the late season. The actual data presented for one year indicate that this effect may have been present but their observations were not continued long enough to see the ultimate reduction. If temperatures were extremely cold, however, no larvae would have been present and it would have been impossible to obtain further data. (2) Their diapause initiation timing is significantly earlier than that obtained in other studies, reaching the 50% level by the middle of August as opposed to October for other locations. North Carolina is further north than the other locations, however, so cooler temperatures and greater changes in daylight period could affect insect behavior.

Less has been reported on HV. Barber (1937) reported that HV appears to enter diapause during a shorter time period than HZ. Phillips and Newsom (1966) found in laboratory experiments that HV was induced into diapause by 10 hr daylight periods at temperatures below 27 C. HV was less sensitive to parental photoperiod experience than HZ. Benschoter (1968) also ran laboratory experiments to investigate the effect of temperature and light level on both HZ and HV. He found a linear increase in percent diapause in HV with decreasing temperature from 27 down to 21 C. Diapause induction was not influenced by light level in either species; however, the rate of development in the larval stage was increased in both species by an increase in light level.

Using outdoor cages, Fye and Carranza (1973) found that HV entered diapause over an 8 week period compared to a 14 week period for HZ. They also found the percent diapause to be much lower in HV, 22% peak, compared to HZ, 50%.

There has been some research on other factors relating to induction of diapause in _H._ spp. For example, Phillips (1969) studied the effect of dietary exposure to plant growth regulators. These chemicals seem to modify diapause, dependant on photoperiod. Thus, the level of diapause may be affected by the type and condition of plants the larvae are feeding on in the fall when the photoperiod becomes favorable.

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Survival through diapause and emergence:

Parencia (1964) introduced larvae into outdoor cages containing two types of soil representative of the central blacklands of Texas. The larvae were obtained from late season host crops each fall and the subsequent emergence of the adult moths was then monitored. Over nine years of trials, the emergence from Houston clay averaged 12.2%, ranging from 0% to 38%. In sandy clay emergence averaged 24.6%, ranging from 0% to 56%. The emergence of moths in the fall from pupae that did not enter diapause was also monitored and it ranged from 0% to 9.6%, 2.1% average, in the clay and from 0.2% to 10.6%, 3.9% average, in the sandy clay.

Rainfall seemed to be the most influencial variable affecting overwinter survival. Dry winters followed by average rainfall in the spring appeared to provide the optimum chance for survival. Excessive moisture in the winter or spring resulted in significant mortality.

Roach (1968) monitored the survival of HZ for two years in an outdoor laboratory. Survival was 86% one year and 92% the next for the diapausing pupal stage. Thus, fairly high survival through diapause is potentially possible.

Slosser et al. (1975) in two years of experiments and two locations studied the effect of temperature, rainfall, solar radiation, and time of year on overwinter survival of HZ. A linear regression model was calculated for cummulative pupal mortality versus number of days, cummulative rainfall, and cummulative hours of temperatures below freezing. The overall regression coefficient was 90%. Partial regression coefficients were 91%, 80%, and 91%, respectively. The percentage of larvae buried that emerged as adults averaged 0.07% at one location and 1.2% at the other over the two years.

Young and Price (1977) studied the survival of HZ in alfalfa, cotton, and grassland in Oklahoma. They included both plowed and unplowed cotton. Plots were sampled monthly, December thru March, and then completely dug up at the end of March to determine emergence number versus time. Monthly average temperatures for December thru March were obtained for the two years. Results from two years averaged 0.32% emergence from alfalfa, 0.19% emergence from pasture, and zero emergence from cotton, whether plowed or unplowed.

Caron et al. (1978) chose to study a native field rather than setting up an artificial situation as others have done. They sampled three locations in North Carolina for HZ in late planted corn. Larval samples were followed through as diapausing pupae and spring emerging adults. The following results were obtained: (1) Percent diapause varied from 21% to 84%, depending on the timing of the pupal population. (2) Survival of diapausing pupae from fall to spring was 8%, 53%, and 20% at the three sites, although sampling problems existed with the first and last because of rocky soil. They feel the 53% is a good estimate for the location with moist, organic soil. (3) The percentage of living pupae in the spring that actually emerged as adults was 2.5%, 19.5%, and 33.4%. Soil crusting was found to greatly affect this percentage.

Laboratory studies by Eger (1981) assessed the mortality during diapause of HZ and HV versus temperature. The model formulation of Casagrande and Haynes (1976) was investigated to describe the results. Good results were obtained for temperatures between -8 and 2 C. Simulations with this model indicate that temperature alone is not a significant factor in the mortality of overwintering HZ and HV in College Station, Tx. Mortalities of only 1 or 2% were predicted for many years tested.

Additional tests were run to assess the effect of moisture and temperature. Moisture significantly increased the mortality. Preconditioning the insects before subjecting them to sub-freezing temperatures was also tested and it appeared to increase the survival. In the field, the burrowing depth of both species was measured and the overwinter survival assessed. For HZ, 1% of the larvae placed in the ground to pupate in the fall emerged in the spring as adults in two years of tests. For HV, 0.0% and C.8% emergence was obtained in the two years.

Supercooling temperatures were also investigated. In earlier work Barber and Dicke (1939) found the freezing point of HZ pupae to be -12.2 C. Ditman et al. (1940 and 1943) found that insects could survive below their freezing points by supercooling. They found the supercooling points for HZ ranged from -14.8 C to -25.4 C depending on food source, humidity, and age of pupae. Salt (1950) found the survival at supercooling levels to be dependent on duration as well. The results of Eger (1981) at supercooling temperatures did not conform to the requirements for the Casagrande-Haynes model formulation. Alternative models will need to be investigated.

Emergence from Diapause:

Mangat and Apple (1966) describe experiments with photoperiod and temperature effects on emergence. They derive a degree-day accumulation of 341 needed above a threshold of 12.6 C for emergence of HZ in Spring. For average conditions in Wisconsin this predicts emergence on June 14 compared with June 19 to July 29 observed emergence. Subsequent research described below has shown that emergence cannot be accurately modeled by the simple degree-day accumulation used for non-diapause development.

Experiments carried out by Wellso (1966) to study the influence of photoperiod on termination did not show any apparent effects for HZ. Chilling HZ pupae to 5.5 C for selected time also had little or no effect. Emergence data was collected for three years at outside temperatures. There appeared to be a tendency for larvae going into diapause first in the fall to be the last to emerge in the spring. He suggests that the temperature threshold for emergence may be affected by the temperature at which they went into diapause. Thus, an insect going into diapause at warmer temperatures earlier in the fall would emerge at later, warmer temperatures in the spring. This "first in -- last out" phenomena was also observed by Fye and Carranza (1973).

Roach (1968), and Roach and Adkisson (1971) present data for two years of emergence of insectory insects experiencing outside conditions. Laboratory studies at various temperatures and photoperiods indicated that photoperiod had little effect. A very low percentage of emergence was obtained at 18 C so any emergence threshold must be near but a little lower than that. They also found that emergence was accelerated by higher temperatures.

Experiments made over two years at two locations in Arkansas are described by Slosser et al. (1975). Multiple linear regression results are shown for cumulative emergence versus day of year, hours of soil temperature above 55 C, radiant energy per day, and rainfall. Soil temperature, radiation, and rainfall were accumulated values from April 1. An overall regression coefficient of 0.964 was obtained. The partial correlation coefficient for rainfall was only 0.208 compared to 0.77, 0.89, and 0.72 for the first three independent variables, respectively. Thus, soil temperature appears to be the primary variable affecting emergence timing. Since radiant energy would directly increase soil temperature, the regression results suggest that timing is a nonlinear function, such as a power function, of temperature.

Andrewartha (1952), Beck (1968), Lees (1955), and Tauber and Tauber (1976), all discuss generalized theories of diapause and, specifically, the importance of temperature as a regulator of processes involved with diapause. Holtzer et al. (1976a) ran a series of temperature experiments. Diapausing insects were held for four time periods, 7, 38, 75, and 111 days, at four temperatures, 3, 8, 13, and 18 C, before moving them to 23 C for final emergence. The total time required for adult emergence was measured for each treatment. Based on the results, they propose two groups of physiological processes involved with diapause emergence, one with maximum rate at low temperature and decreasing at higher temperatures (above 18 C.), the second with maximum rate above 18 C and decreasing below 18 C. Thus diapausing insects would require some time at low temperatures to complete the one type of development and time at higher temperatures to complete the other type of development.

Holtzer et al. (1976b) also carried out a series of breeding experiments with two initial strains of HZ, one from North Carolina and one from Florida. Mating was controlled within each strain to select for one group having low emergence time and another having long emergence time. All rearing and diapause was carried out under a fixed program of photoperiod and temperature. The initial difference between the NC and FL strains was 9.1 days, which was significant statistically. The groups bred for shortest emergence time did not achieve times which were significantly different than the original parent stock. The groups bred for longest time achieved significantly longer diapause emergence times, 70 to 80 days, after two generations versus 36 to 45 days for the parent stock. It appears that the initial strains collected in the field were adapted to the shortest time possible for the species. Genetics does seem to play a definite part in determining diapause behavior and may need to be considered in modeling emergence.

The biochemical processes which take place during diapause and lead to the resumption of morphogenic development were termed "diapause development" by Andrewartha (1952). Based on the results of Holtzer et al. (1976a), Logan et al. (1979) formulated a model for HZ diapause development, having two phases. Phase I is true diapause development with the optimum rate at temperatures below the diapause threshold. Once the diapause state is completed, the insect goes into a "refractory" state, Phase II, ready to complete pupal morphogenic development. They hypothesize that Phase II is similar to non-diapause pupal development except for the value of the developmental temperature threshold. (Note: the word "refractory" is also used by other authors to refer to behavior in Phase I.)

Data from Holtzer et al. (1976a) indicate that Phase I is completed in ca. 38 days at 13 to 18 C. In North Carolina this phase would therefore be completed before temperatures are warm enough to exceed the Phase II threshold. Thus, Logan et al. (1979) developed a quantitative model for Phase II only.

Experiments with laboratory insects were used to calibrate the model. They measured pupal depth and fit an "extreme value" distribution. Soil temperature was also measured and used to develop a model for temperature versus time and depth. Regression results with the model of pupal development in Phase II resulted in a development threshold of 15 C.

Wilson et al. (1979) develop a similar model for emergence of HA. It extends the model of Logan et al. (1979) in that Phase II is seperated into two parts: first a "reactivation" period and second the true pupal morphogenic development stage, identical to non-diapausing pupae. Diapausing HA pupae were sequentially sampled through the winter and held at 26.7 C. Times to diapause termination and to subsequent moth emergence were measured. Timing of diapause termination and emergence was also measured at 18, 22, 26, 30, and 35 C. From these data a quantitative emergence model was derived. Development of the pupae after termination of diapause was found to follow the same degree-day formula with threshold at 12.5 C that is used in population dynamics models for HZ and HV (Hartstack et al. 1976). Timing of the reactivation period of diapause was modeled with a separate degree-day accumulation using a nonlinear function with threshold at 17 C. As with Holtzer et al. (1976a) this model presupposes that timing of entry does not affect timing of emergence in the spring. Once diapausing pupae recieved sufficient cool exposure in Phase I, they enter a single queue awaiting favorable conditions for emergence. The condition for emergence is the accumulation of sufficient warm temperatures above 17 C to complete the reactivation process. A geometric distribution was found to be a suitable description of the variation in time to break diapause. This distribution was fit to the results at the various emergence temperatures.

Most lepidopterous spp. appear to have an initial stage upon entry into diapause from which they do not immediately emerge when put into warmer temperatures (Andrewartha 1952). This initial phase of diapause is referred to by some as "refractory" (Meola and Adkisson 1977). Once this refractory state is completed, they then seem to go into a holding pattern from which they will directly emerge out of diapause once in warmer temperature. Experiments with these insects show that placing them in cold temperature will, in fact, speed up the completion of the refractory period. Such behavior matches with the hypothesis model of Holtzer et al. (1976a) described above.

Several researchers have shown, however, that chilling is not required in HZ to accelerate diapause termination as in other insects (Phillips and Newsom 1966 and Wellso 1966). Experiments by Meola and Adkisson (1977) indicate that diapause in HZ is not due to the hormonal deficiency common to other Lepidoptera. They suggest, then, that HZ does not have an initial refractory phase of diapause; rather, termination is in direct response to temperatures above 21 C.

The lack of a quantitative model describing the transition process into diapause and the initial phase of diapause, leaves some question about the experimental designs used in the reported chilling research. If, for example, the test insects had completed the first stage, then no chilling effects would be expected. Further research would appear to be required to more completely define Phase I behavior.

Again, less research has been reported on HV. Fife and Graham (1966) monitored the spring emergence of both HZ and HV near Brownsville, Tx. They reported that 73% of the overwintering HV emerged in March compared to 65% of the HZ in April. Current research in the College Station, Tx. area is finding similar results. Apparently there are significant differences in the pattern of emergence from diapause between the two species.

CURRENT RESEARCH IN DIAPAUSE SIMULATION

Initiation of Diapause:

Day Length -- Many researchers have reported that decreasing daylight period, together with decreasing temperature, is the signal that causes HZ and HV to switch into the overwintering diapause state rather than continuing normal development. Diapause initiation begins at College Station around September 20, on the average, and reaches a peak about October 20. During this period around the Equinox, photoperiod is changing at its maximum rate.

After reaching a peak in late October, the percentage of insects going into diapause begins to decrease, concurrent with the decrease in the change of photoperiod from one day to the next. Apparently, by late November, very few HZ and HV initiate diapause. Insect behavior is difficult to quantify in the field at this time because very few larvae, if any, actually reach the pupal stage due to cool temperatures.

Temperature -- Temperature interacts with photoperiod to affect diapause behavior. Very low diapause initiation will occur above temperatures of 23 C regardless of photoperiod. Once temperatures go below 23 C in combination with shortening daylight period, diapause initiation will increase as temperatures become lower, reaching a maximum at temperatures below 17 C.

Temperature also affects oviposition by HZ and HV females. Maximum oviposition occurs at ca. 24 C and decreases to practically zero at 17 C. Therefore, very few eggs would be laid in the field at College Station after November 1.

Fig. 1 shows the accumulated degree days from September 1 to December 31 for 1980. The horizontal lines define degree-days required for completion of the various life stages of HZ and HV. A typical diapause initiation curve has also been added to Fig. 1 using the larva-to-pupa transition as a baseline. Tracing the developmental curves back to the egg stage, one can see that the individuals going into diapause between September 30 and November 20 originated from oviposition between September 5 and October 10. Any oviposition after October 10 would not have sufficient time to enter diapause because of low temperature and decreasing change in photoperiod. Moreover, the majority of the diapausing pupae would have come from oviposition between September 15 and October 1, a 15 day period. Thus, determination of the timing of both fall populations and diapause initiation will be extremely critical in determining the number of insects that will emerge in the spring.

Survival through Diapause and Emergence:

Some progress has been made in determining the effect of temperature, moisture, soil type and field tillage on pupal mortality. It appears that the majority of the overwintering pupae that survive are located in field boundaries, meadows, pastures and along ditch and stream banks where they are undisturbed by field operations. However, recent, unpublished work by Roach indicated good moth emergence from cultivated areas. Large numbers are evidently destroyed by predators such as birds and small animals. Accurate prediction of overwintering mortality is therefore going to be difficult.

Emergence from Diapause:

The pattern of emergence from diapause is assumed to be primarily controlled by temperature. Based on the earlier work of Holtzer et al. (1976a), Logan et al. (1979), and Wilson et al. (1979), the diapause sequence has been conceptually divided into three stages as depicted in Fig. 2. The initial stage is the transition period into diapause. Much research has centered on the environmental triggers and timing of the transition. It is evident that larvae are "programmed" for possible diapause by environmental conditions over a period of time. Definition of the transition mechanism is incomplete, however, as are the requirements which determine whether or not the transition is successfully completed.

The second period represents the "true diapause" period. Biologic processes leading to the completion of this stage appear to be somewhat independent of temperature, but may slow for temperatures near or below freezing. HV evidently complete this period by late December in the College Station area (Lopez et al. 1981).

The third stage is the transition out of diapause, termed the "reactivation" stage by Wilson et al. (1979). Timing appears to be determined by the insect recieving sufficient exposure to temperatures above a fixed threshold. Upon completion of the third stage, diapause is broken and the insect enters the pupal development stage, comparable to non-diapausing pupae. Once this development is complete, the adult moth emerges from the ground.

Obvious differences exist between HZ and HV in the termination of diapause, however, for our initial model we assume a similar model structure for both and plan to include any differences later as sufficient data are available.

The two stage emergence sequence (reactivation period followed by normal pupal development) has been substantiated to some degree by field data. The model by Wilson et al. (1979) was based on data collected for HA. Lopez et al. (1981) found a similar relationship existed for HV (Table 1). Pupae collected in January and Feburary were all in diapause and when subjected to 26.7 C they emerged in ca. the same length of time. Thus, they appeared to be queued, waiting for warm temperatures above the reactivation threshold. Pupae collected after Feburary were beginning to break diapause and the variation in emergence time began to increase the later they were collected. This increase in variation of emergence time is very likely due to a variation in the location of each pupa in the soil -- shallow, deep, under crop residue, top of furrow or bottom of furrow -- which altered the amount of heat units each pupa recieved. The longer they remained in the soil, then, after the air temperature was above the diapause threshold, the more variation occurred.

Breaking Diapause -- Wilson et al. (1979) also reported that the temperature threshold for HA during the reactivation period was 17 C and the effect of higher temperature was not linear but exponential. The data of Lopez et al. (1981) confirmed that HV reacted similarly, however, the threshold was calculated to be 21 C. Since air temperature was used instead of soil temperature, it was assumed that this difference probably accounts for the 4 C difference in threshold temperatures. Accordingly, the following equation is used to calculate hourly heat units, DDG:

$$\begin{aligned} DDG &= EXP(1.7 * LOG(T - 21)) && \text{for } T > 21\text{ C} \\ DDG &= 0.0 && \text{for } T < 21\text{ C} \end{aligned} \qquad (1)$$

where
T = Hourly air temperature.

This function for rate of development is shown in Fig. 3. The hourly heat units are accumulated and divided by 24 to convert to degree-days (DD). The mean time for breaking diapause occurs when 70 DD have been accumulated. At this time the pupae begin normal development.

Post Diapause Development -- Wilson et al. (1979) found that after diapause was broken, the rate of development for HA pupae was similar to non-diapausing pupae. Our field data indicated the same results; therefore, the model from MOTHZV (Hartstack et al. 1976) was used:

$$\begin{aligned} DDP &= (T - 12.6) && \text{for } 12.6 < T < 33\text{ C,} \\ DDP &= 0.0 && \text{for } T < 0.0\text{ C or } 53.4\text{ C} < T, \\ DDP &= (53.4 - T) && \text{for } 33 < T < 53.4\text{ C,} \end{aligned} \qquad (2)$$

where
DDP = hourly heat units
T = hourly air temperature.

This linear relationship is shown in Fig. 3. As above, the hourly heat units are accumulated and divided by 24 to predict the completion of pupal development. The mean time for completion is 179.5 DD.

Emergence Distribution Over Time -- The field data in Table 1 shows that the emergence of the pupae collected in January and February was distributed over an 8 to 10 day period. It would be difficult to seperate this variation between development before breaking diapause and development after breaking diapause. Therefore, our model simulates this variance at the time they emerge as adults. Sharp et al. (1977) suggested a method for handling distributions of organism developmental times which we have found appropriate for HZ and HV. This method is based on the assumption that the rate of development is normally distributed around the mean, resulting in a skewed distribution for the reciprocal, time of development.

As stated earlier 179.5 DD are required for the pupae to develop and emerge. To use this method of distributing emergence, development is converted to physiological days rather than calendar days. One physiological day is assumed to be 14.45 DD, based on the accumulated development for one day at a temperature of 26.7 C. Dividing 179.5 by 14.45 yields 12.42 physiological days needed for development of non-diapausing pupae. A normal distribution is used to describe the rate of development, centered on the inverse of 12.42 days (0.0805). This is shown in Fig. 4 together with the resulting inverse distribution for days to emergence.

Predicted values for standard deviation are relatively constant (0.0066) until the end of February when they begin increasing, reaching a value of 0.03 or larger at the time of natural emergence in the field. The reason for this increase in variation was explained earlier.

It is assumed that all diapausing pupae in the reactivation queue break diapause on the same day and begin seasonal non-diapausing development as temperature requirements are met. The prediction of emergence is then distributed over time with the technique just explained. Figs. 5a and 5b present a comparison of the predicted emergence against the observed emergence in the laboratory for individual cohorts collected on January 3, February 6, March 7 and April 11. Fig. 6 shows the predicted emergence compared to that observed in field cages. The mean day of emergence in the cages was 115.8 and the predicted was 114.0.

Predicting Trap Catch -- Emergence of HZ and HV in the field is very difficult to measure since the number of overwintering pupae is low and they are distributed over the entire area where host plants were available in the fall. Pheromone traps (Hartstack et al. 1979) are an excellent monitoring device for male HZ and HV, especially in the spring and early summer before large numbers of females begin to compete with the trap for males. Trap catches are not a direct measure of emergence since moths live a number of days when the temperature is mild. Therefore, the catch on any one night represents the active population of males of various ages.

Moth activity is determined primarily by temperature and has been measured for HZ and HV (Hartstack et al. 1978). Based on those results, moth activity can be estimated as follows: An hourly activity function, ACT, is calculated for each hour from 8 pm through 6 am as

$$ACT = -44.45 + T * (5.3 + T * (-0.20154 + T * 0.00248)) \qquad (3)$$

where

T = Four hour exponential average temperature.

Daily percent activity is then obtained as the average of the hourly function over the 11 hour period each day.

A portion of MOTHZV (Hartstack et al. 1976) can be used to determine longevity and mortality of adults. The predicted percent emergence, as calculated above, is multiplied by a constant (1000) to obtain a nominal number of new moths to input to the simulation model. This daily input is stored and the number reduced for mortality. The temperature activity function is used to estimate the percent of the moth population which will be active for possible trap catch. The number remaining after mortality deductions, are kept and added to the new emergence for the next day. This procedure continues until the emergence is complete.

The number of active moths each day and the predicted pheromone trap catch are normalized to a peak value of 1.0 for printout. Figs. 7a and 7b show the comparison of predicted versus observed trap catch for 1978 through 1980. Table 2 presents the emergence in cages for 1980 and the field traps catches for 1978 through 1980. It is obvious that the predicted trap catch does not exactly match the measured catch in any year. There are many complicating factors which remain to be resolved such as migration, rainfall, and host plant patterns.

Predicting Future Generations:

The predicted emergence frequency distributions can be entered into MOTHZV for initiation of simulations to predict timing of future generations through a complete crop season. The predicted percent emergence is multiplied by 1000 to obtain an integral number of moths. The model, MOTHZV as described by Hartstack et al. (1976) and Hartstack and Witz (1980) can predict timing of future moth flights (or egg peaks) with accuracy. Fig. 8 through Fig. 10 show the predicted moth numbers compared to pheromone trap catches in 1978 through 1980, respectively. If these trap catches reflect actual populations (Hartstack et al. 1981), then the emergence model along with MOTHZV did an extremely good job in predicting the July peak each year. This period is of major importance with regard to the potential damage to cotton.

POTENTIAL USE OF HELIOTHIS MODELS IN EARLY WARNING

Integrated pest management (IPM) systems for control of H. spp. involving the use of beneficial insects, microbial agents, sterile insect releases, insecticides, pheromones, resistant varieties and cultural practices are being recommended by agricultural scientists throughout the world. One of the key factors in making any IPM program workable is an accurate measure of the size of the pest insect population. Most large scale control or management systems work best when populations of the pest insect are low. This is especially true when trying to deal with the <u>H.</u> spp. They are usually at their lowest level in the spring, during emergence of adults that have overwintered in diapausing conditions. Traps do offer a means of measuring the population; however, they are expensive to operate and would require extensive resources to cover large areas. If the size and timing of spring populations could be predicted with reasonable accuracy, large scale programs could be carried out to reduce these potential pests to extremely low numbers. Such early season programs could perhaps eliminate any need for control of these pests in later generations or at least reduce such needs to minor control programs which could utilize methods other than insecticides. Early population predictions might also separate years when no controls would be necessary from years when large programs would be required.

ADDITIONAL RESEARCH REQUIREMENTS NEEDED FOR EARLY WARNING SYSTEM

<u>Initiation of Diapause</u>:

Some factors controlling diapause initiation have been reported and their effect has been shown. However the interaction of these factors, particularly photoperiod and temperature, has not been completely documented. This interaction appears to affect the percentage of pupae that go into diapause as well as how firm they might be in diapause. The timing of diapause initiation in pupae becomes quite critical when one is concerned with the timing and size of the preceeding life stages. It appears that 60 to 70% of the diapause programmed pupae might originate from eggs laid over only a 15 day period. This reveals the need to be able to monitor adult populations very closely during this time and be able to predict which eggs will become potential diapause programmed pupae.

The following specific research tasks are needed: (1) Develop a model which will accurately convert pheromone trap catches to actual field population densities, specifically during the time when eggs are potentially destined to develop into diapausing pupae. (2) Evaluate the interaction between photoperiod and temperature to enable prediction of timing and percent of eggs laid that will develop into diapausing pupae. (3) Determine if the timing or conditions of diapause initiation have an influence on the timing of adult emergence in spring. (4) Develop a method to determine the condition and abundance of fall host plants. The stage and condition of the host determine the oviposition and the survival of eggs and larvae. Remote sensing of vegetational condition needs to be investigated in order to provide wide area conditions.

<u>Overwintering Survival of Diapausing Pupae</u>:

Many factors are known to cause mortality of diapausing pupae. The effect of temperature has been well documented and a model developed. Research on the following factors is needed: (1) The effect of soil moisture and rainfall (amount and intensity) on survival. (2) The effect of ground vegetation on survival. (3) The effect of general soil types, in conjuction with soil moisture, on survival. (4) Correlations between remote sensing data and soil moisture, vegetation, soil types and soil temperature should be investigated for possible clues to mortality rates. (5) The effect of biotic mortality factors such as predators or parasites.

Emergence from Diapause:

Considerable progress has been made by this unit over the past 2 years in developing a model that predicts the timing of H. spp. spring emergence. Comparisons have been made between predictions and actual emergence of adults in cages (tables 1 and 2). Similar information is being collected in 1981 for both HZ and HV. Hopefully, this will provide sufficient data for model validation. Additional research needs are: (1) Determine the relationship of air temperature to soil temperature under various vegetative canopies. Develop methodology to obtain wide area soil temperature data from remote sensing data bases and integrate such data with a H. spp. emergence prediction model. (2) Develop methodolgy to obtain wide area estimates of early spring host plant availability and condition. Integrate such estimates with the H. spp. emergence prediction model. (3) Determine the relationship between rainfall and emergence of adults, both as to mortality and timing of emergence.

Long Range Migration:

This report has dealt specifically with the diapause mechanism for overwinter survival of H. spp. However, as mentioned at the opening, local infestations may also occur due to long range migration of H. spp. adults. Spring trap catch data taken in conjunction with diapause research at several locations have left some questions as to the actual origin of the captured moths. Thus, it appears that migration will need to be considered as an integral part of the overwintering survival and spring infestation of H. spp.

Long range migration of H. spp. adults has created much discussion among scientists. The adults are strong fliers and have been shown to cover distances of at least 100 miles without stopping (Sparks 1979). If the adults were assisted by strong air currents, they could concievably move hundreds of miles in 24 hours and infest areas far from the site where they developed. Parencia (1964) observed that HZ were present and completed a full generation at Waco, Texas, before the local overwintering moths emerged. The early spring population was evidently due to migration.

If a significant portion of a local population derives from migration, then predictive capability for such migration will need to be included in any early warning system based on early spring populations. Thus research is necessary to determine the actual extent of long range migration of H. spp. and the part it plays in determining pest populations in crop production regions.

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Table 1. The Adult Emergence of <u>Heliothis</u> <u>virescens</u> Pupae Removed From Soil and Placed at 26.7 C (Lopez et al. 1981).

Adult Emergence	Date Cohort Removed from Soil															
Timing	Dec.	Jan.			Feb.				Mar.			Apr.				May
(Days)	10	3	16	25	6	15	21	28	7	14	20	2	11	17	26	8
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1
1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	2
2	0	0	0	0	0	0	0	0	0	0	0	2	3	3	2	0
3	0	0	0	0	0	0	0	0	0	0	1	0	3	4	3	1
4	0	0	0	0	0	0	0	0	0	0	0	3	12	4	3	1
5	0	0	0	0	0	0	0	0	0	0	2	5	4	4	2	1
6	0	0	0	0	0	0	0	0	0	0	0	9	7	2	2	0
7	0	0	0	0	0	0	0	0	0	0	3	2	4	6	3	1
8	0	0	0	0	0	0	0	0	0	1	3	2	4	4	2	1
9	0	0	0	0	0	0	0	0	0	1	1	4	3	6	1	0
10	0	0	0	0	0	0	0	0	0	1	1	6	4	8	1	0
11	0	0	0	0	0	0	1	1	3	3	3	5	5	3	0	1
12	0	0	0	0	0	0	0	0	5	4	7	6	3	6	0	0
13	2	1	3	1	0	0	1	1	5	4	6	7	3	0	0	0
14	0	7	16	11	21	9	4	7	11	9	6	11	2	3	0	0
15	0	12	21	19	21	12	16	21	20	8	11	10	4	2	2	0
16	1	24	21	25	37	19	11	9	21	8	24	21	4	3	0	0
17	4	8	12	11	20	22	16	18	20	6	15	13	1	1	0	0
18	3	13	3	9	13	12	8	8	11	2	13	7	1	0	0	0
19	3	2	3	0	6	8	7	6	5	1	10	1	1	0	0	0
20	5	2	0	0	2	2	4	1	0	1	0	0	0	0	0	0
21	9	1	0	0	1	1	3	0	0	0	0	0	0	0	0	0
22	7	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
23	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mean Emerg. Length (Days)	21	16	16	16	16	17	17	16	16	14	15	13	9	8	6	4

Table 2. Emergence of Adults in 6 ft. X 6 ft. Screen Cages Placed on Top of Overwintering Sites of *Heliothis virescens* Pupae and Pheromone Trap Catches of Adult Males at College Station, Texas.

Day-of-Year	Adult Emergence in Cages			Pheromone Trap Catch \1		
	Male	Female	Total	1980	1979	1978
70	.0	.0	.0	.0	.0	.0
71	.0	.0	.0	1.0	.0	.0
72	.0	.0	.0	1.1	.0	.0
73	.0	.0	.0	1.0	.0	.0
74	.0	.0	.0	.0	.0	.0
75	.0	.0	.0	.1	.0	.0
76	.0	.0	.0	1.0	.0	.0
77	.0	.0	.0	.0	.0	.0
78	.0	.0	.0	.0	.0	.0
79	.0	.0	.0	.0	.0	.0
80	.0	.0	.0	.4	.1	.0
81	.0	.0	.0	.4	.0	.0
82	.0	.0	.0	.6	.0	.0
83	.0	.0	.0	.8	.0	.0
84	.0	.0	.0	.1	.2	.0
85	.0	.0	.0	.0	.1	.0
86	.0	.0	.0	.7	.0	.0
87	.0	.0	.0	1.0	.1	.0
88	.0	.0	.0	.2	.1	.0
89	.0	.0	.0	.2	.0	.0
90	.0	.0	.0	.6	1.3	.0
91	.0	.0	.0	1.1	.5	.0
92	.0	1.0	1.0	4.5	1.6	.0
93	.0	.0	.0	1.8	.0	.0
94	.0	.0	.0	1.5	.4	.3
95	.0	1.0	1.0	2.2	.6	.0
96	.0	.0	.0	2.2	.3	.6
97	.0	.0	.0	2.6	1.8	.0
98	1.0	4.0	5.0	4.1	3.1	.0
99	1.0	4.0	5.0	1.2	1.9	.5
100	.0	1.0	1.0	.4	2.2	.0
101	.0	.0	.0	6.1	3.1	.0
102	.0	.0	.0	6.9	2.4	.0
103	2.0	.0	2.0	.4	2.1	.6
104	.0	.0	.0	.1	3.3	.2
105	.0	.0	.0	.5	4.1	.0
106	.0	.0	.0	1.4	13.2	1.0
107	1.0	3.0	4.0	3.1	11.7	2.4
108	1.0	4.0	5.0	3.0	11.5	.9
109	2.0	2.0	4.0	3.6	10.9	.4
110	1.0	1.0	2.0	4.0	9.7	.9

Table 2. (Continued)

Day-of-Year	Adult Emergence in Cages			Pheromone Trap Catch \1		
	Male	Female	Total	1980	1979	1978
111	5.0	5.0	10.0	5.3	12.1	.8
112	.0	3.0	3.0	12.1	8.6	1.4
113	.0	2.0	2.0	21.4	5.7	2.2
114	1.0	1.0	2.0	20.9	7.3	2.9
115	1.0	5.0	6.0	30.3	13.5	.5
116	5.0	2.0	7.0	7.6	4.9	.7
117	.0	.0	.0	4.8	10.7	1.2
118	.0	.0	.0	4.8	9.6	.8
119	.0	.0	.0	9.4	6.7	1.6
120	3.0	3.0	6.0	24.4	8.4	1.9
121	2.0	3.0	5.0	27.0	8.0	3.1
122	1.0	2.0	3.0	13.6	14.3	.0
123	2.0	1.0	3.0	13.4	2.7	.0
124	2.0	2.0	4.0	13.8	2.1	1.6
125	.0	.0	.0	13.5	6.5	.6
126	1.0	1.0	2.0	13.1	9.2	1.6
127	1.0	5.0	6.0	16.5	7.8	3.9
128	3.0	7.0	10.0	10.6	10.0	3.3
129	4.0	2.0	6.0	7.9	16.7	4.4
130	1.0	.0	1.0	9.3	15.6	2.3
131	1.0	.0	1.0	10.0	1.6	1.9
132	.0	1.0	1.0	11.8	4.0	3.5
133	2.0	1.0	3.0	10.0	7.9	.3
134	.0	.0	.0	2.6	10.5	.9
135	.0	.0	.0	3.3	18.4	1.4
136	.0	.0	.0	1.6	18.2	1.5
137	.0	.0	.0	2.3	17.6	1.3
138	.0	.0	.0	2.4	19.8	1.8
139	1.0	2.0	3.0	3.0	21.0	.4
140	.0	.0	.0	2.7	20.9	.8
141	.0	.0	.0	4.0	3.9	.7
142	.0	.0	.0	3.7	1.7	.5
143	.0	.0	.0	2.1	6.1	.5
144	.0	.0	.0	3.3	1.7	.3
Mean Day of Emergence or Trap Catch	115.8	118.2	117.0	119.2	123.7	123.5
Mean Catch per Trap-Night				2.8	2.9	0.4

\1 - The TP-50-75 trap was used in 1978,
the TP-75-50 trap was used in 1979 and 1980.

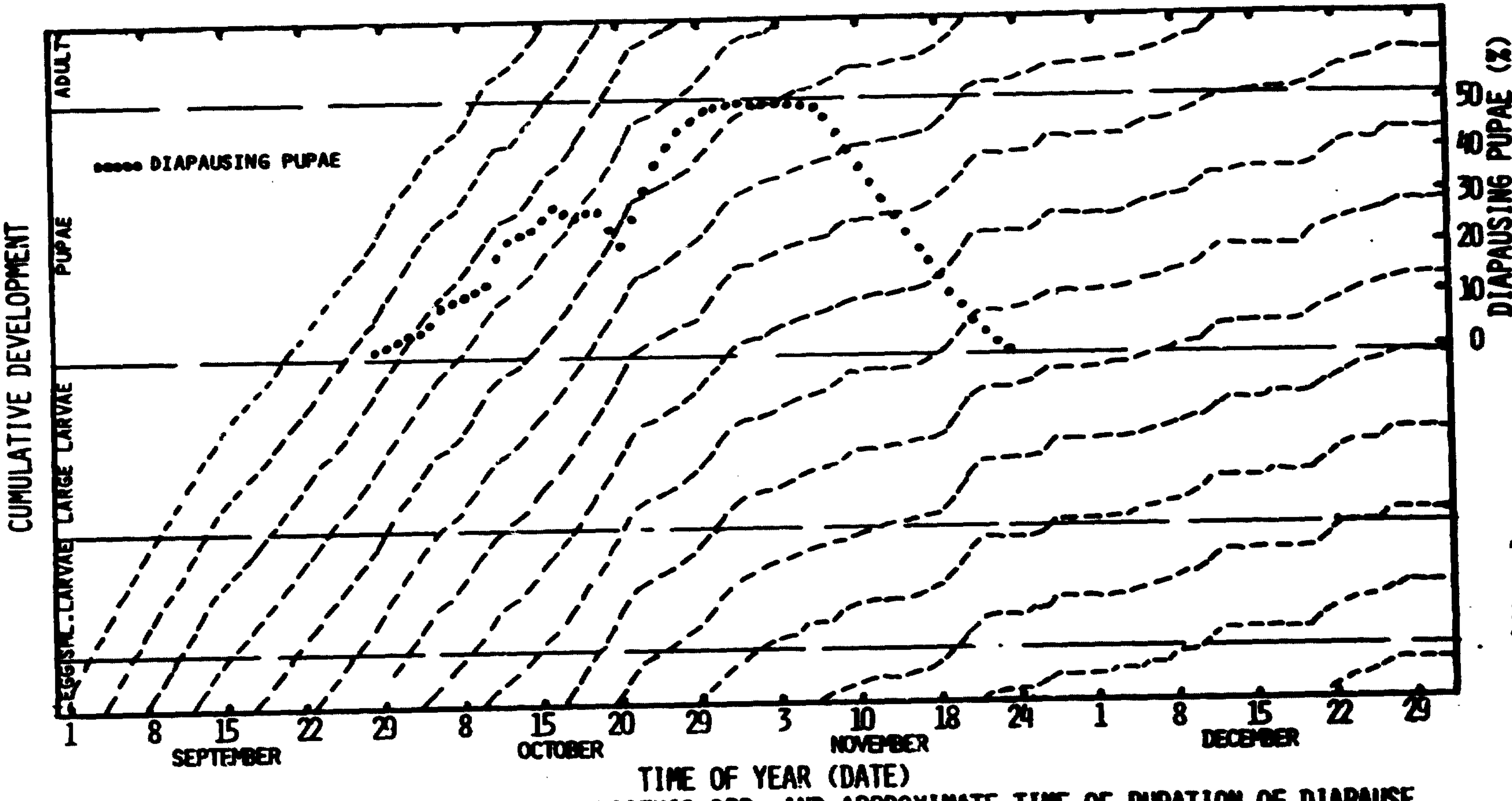

FIG. 1. CUMULATIVE DEVELOPMENT OF HELIOTHIS SPP. AND APPROXIMATE TIME OF PUPATION OF DIAPAUSE PROGRAMMED LARVAE IN FALL OF 1980 AT COLLEGE STATION, TEXAS.

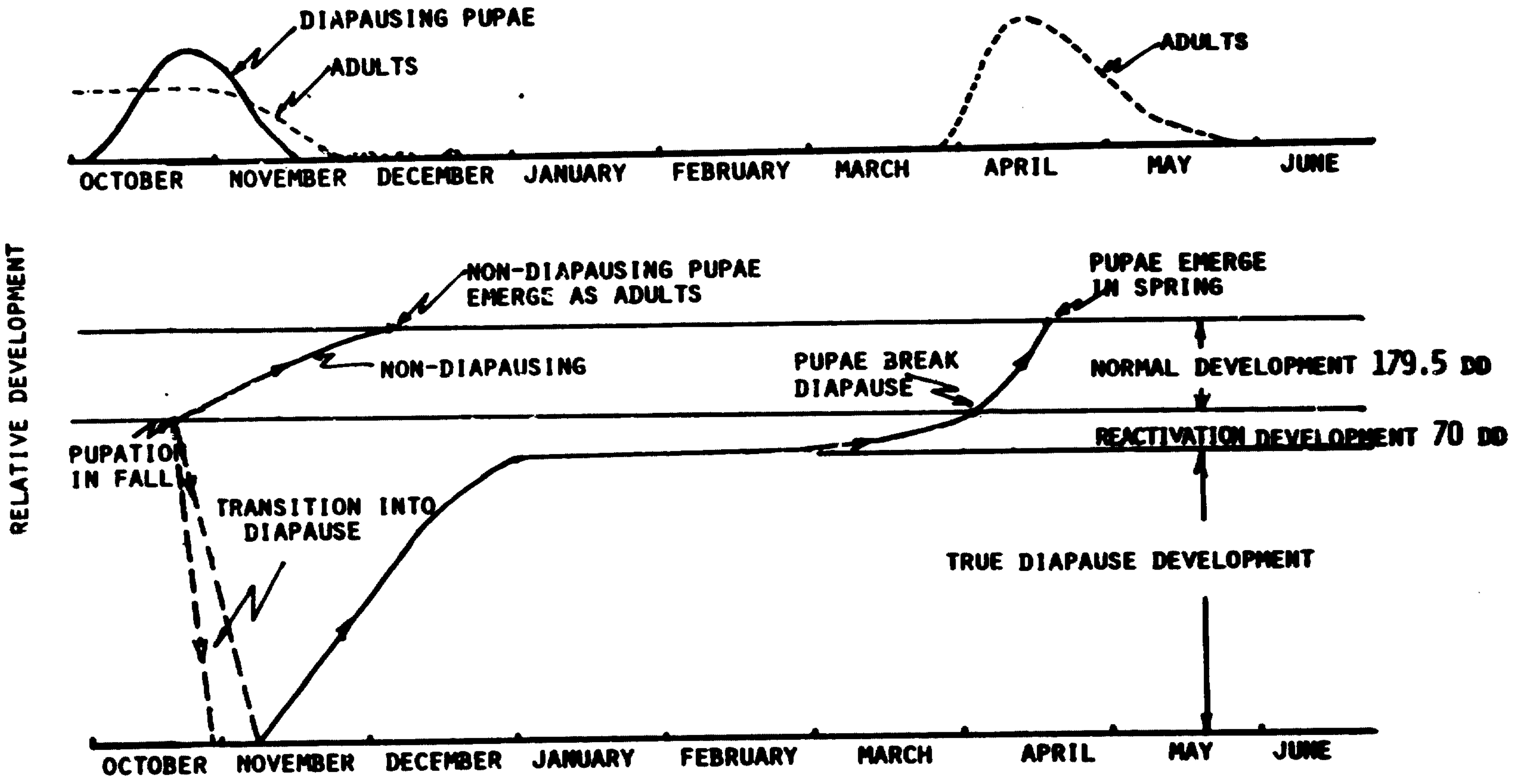

FIG. 2 . CONCEPTUAL MODEL OF DIAPAUSE OF <u>HELIOTHIS</u> SPP.

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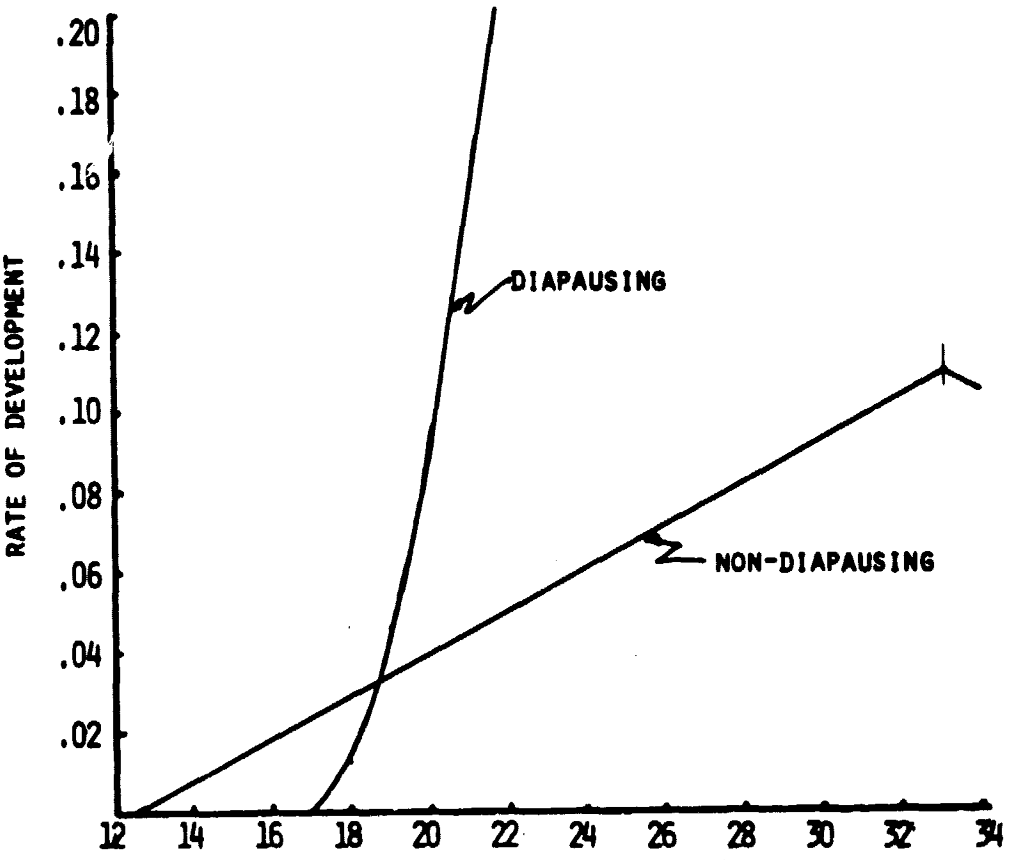

FIG. 3 . RATE OF DEVELOPMENT BY PUPAE

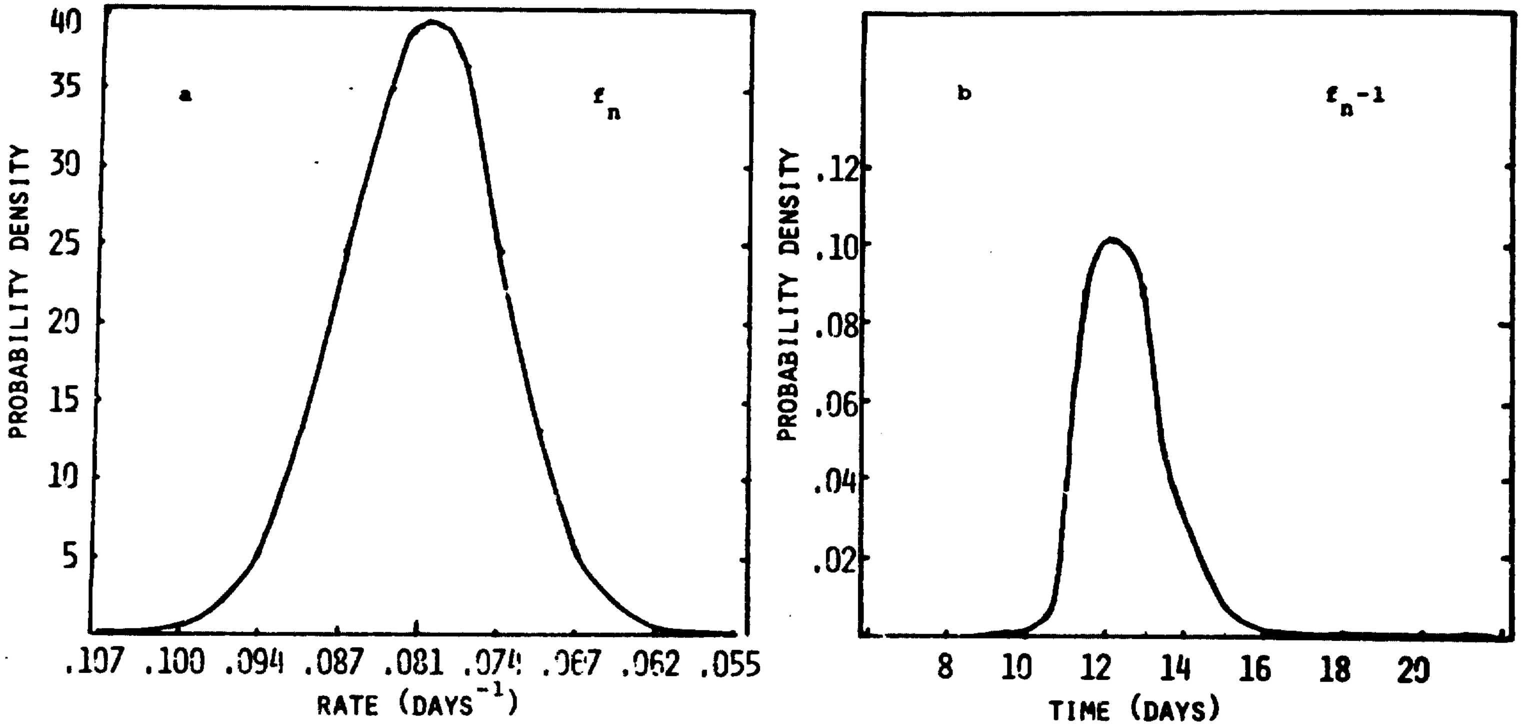

FIG. 4 . NORMAL FUNCTION (a) AND ASYMMETRIC RECIPROCAL (b) FUNCTION. THE f_n AND f_n^{-1} FUNCTION SHOWN FOR μ = .0805 DAY σ = .0066.

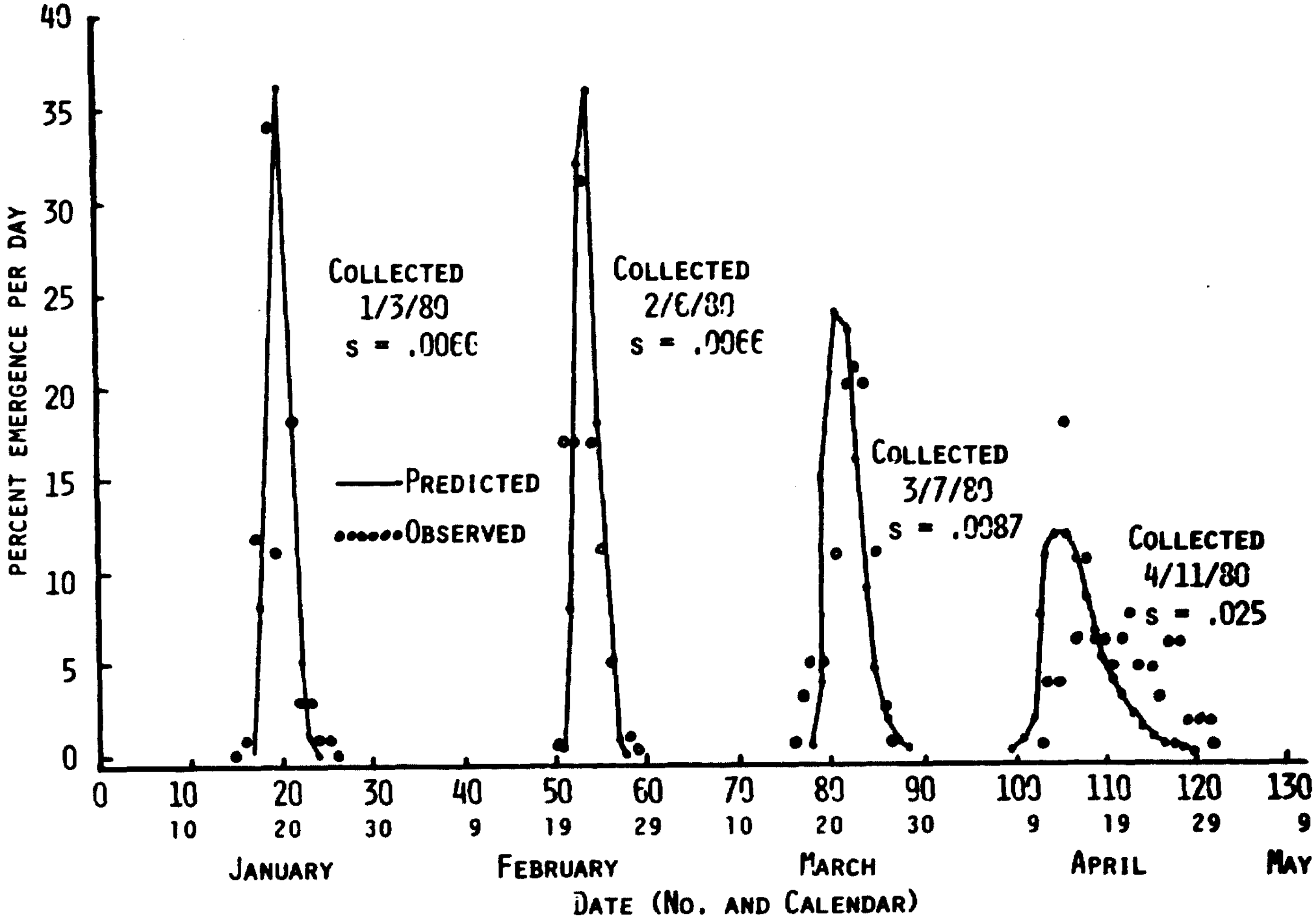

FIGURE 5A. OBSERVED EMERGENCE FROM COHORTS COLLECTED FROM THE FIELD ON VARIOUS DATES COMPARED TO PREDICTED EMERGENCE BY THE MODEL.

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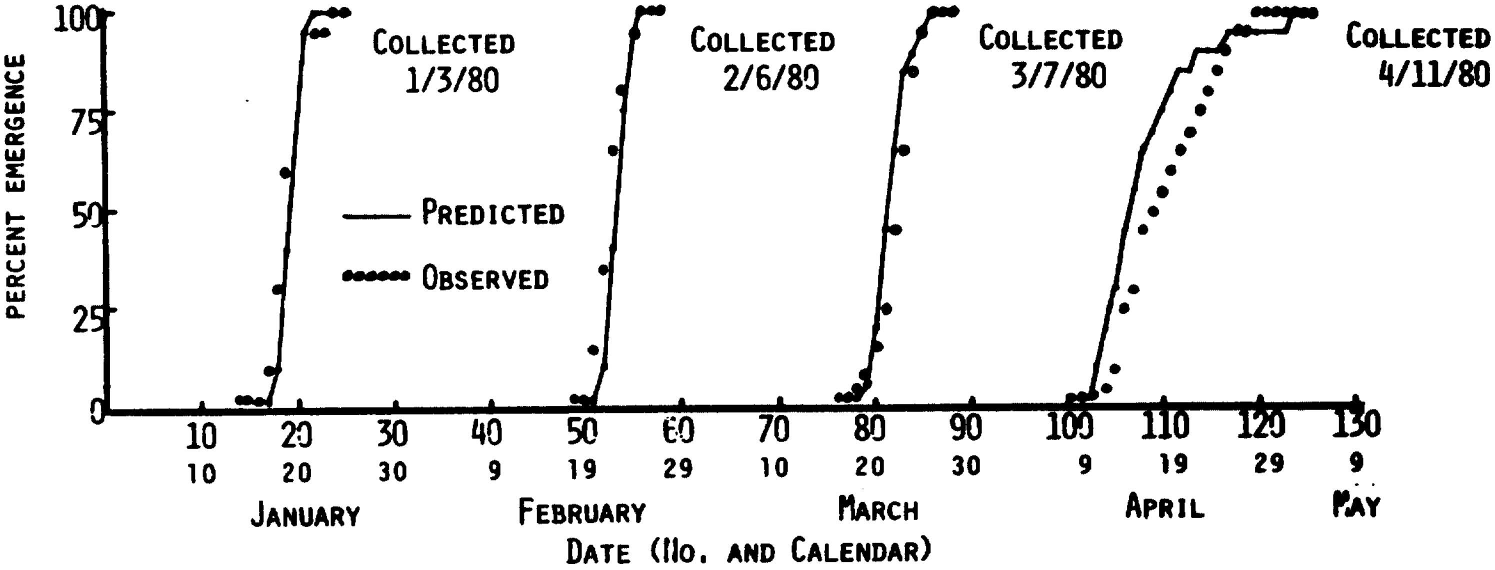

FIGURE 5B. THE ACCUMULATED OBSERVED AND PREDICTED EMERGENCE FROM COHORTS COLLECTED FROM FIELD ON VARIOUS DATES.

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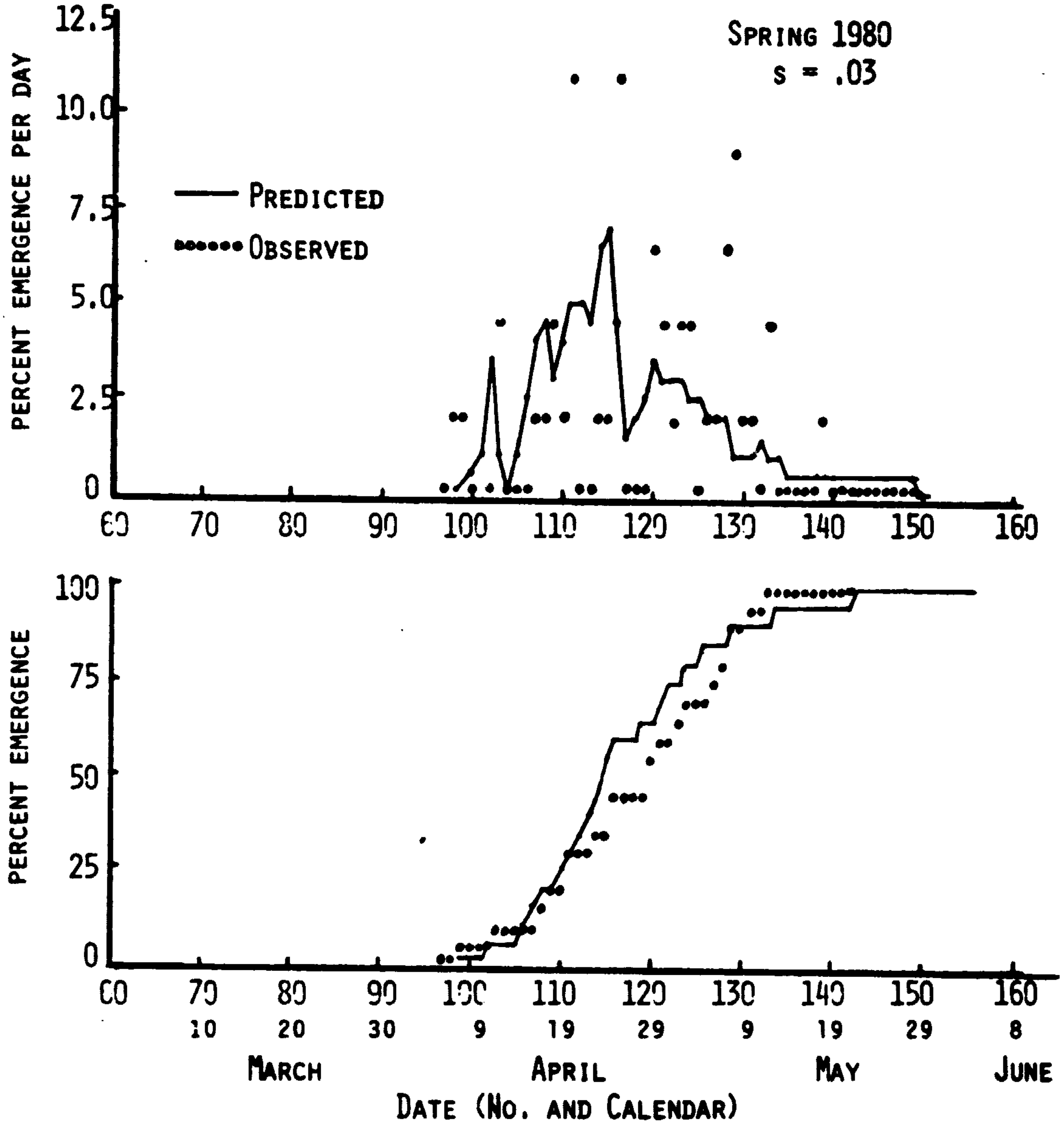

FIGURE 6. OBSERVED EMERGENCE OF MALES IN CAGES PLACED OVER FIELD SITES OF DIAPAUSING PUPAE COMPARED TO PREDICTION BY MODEL.

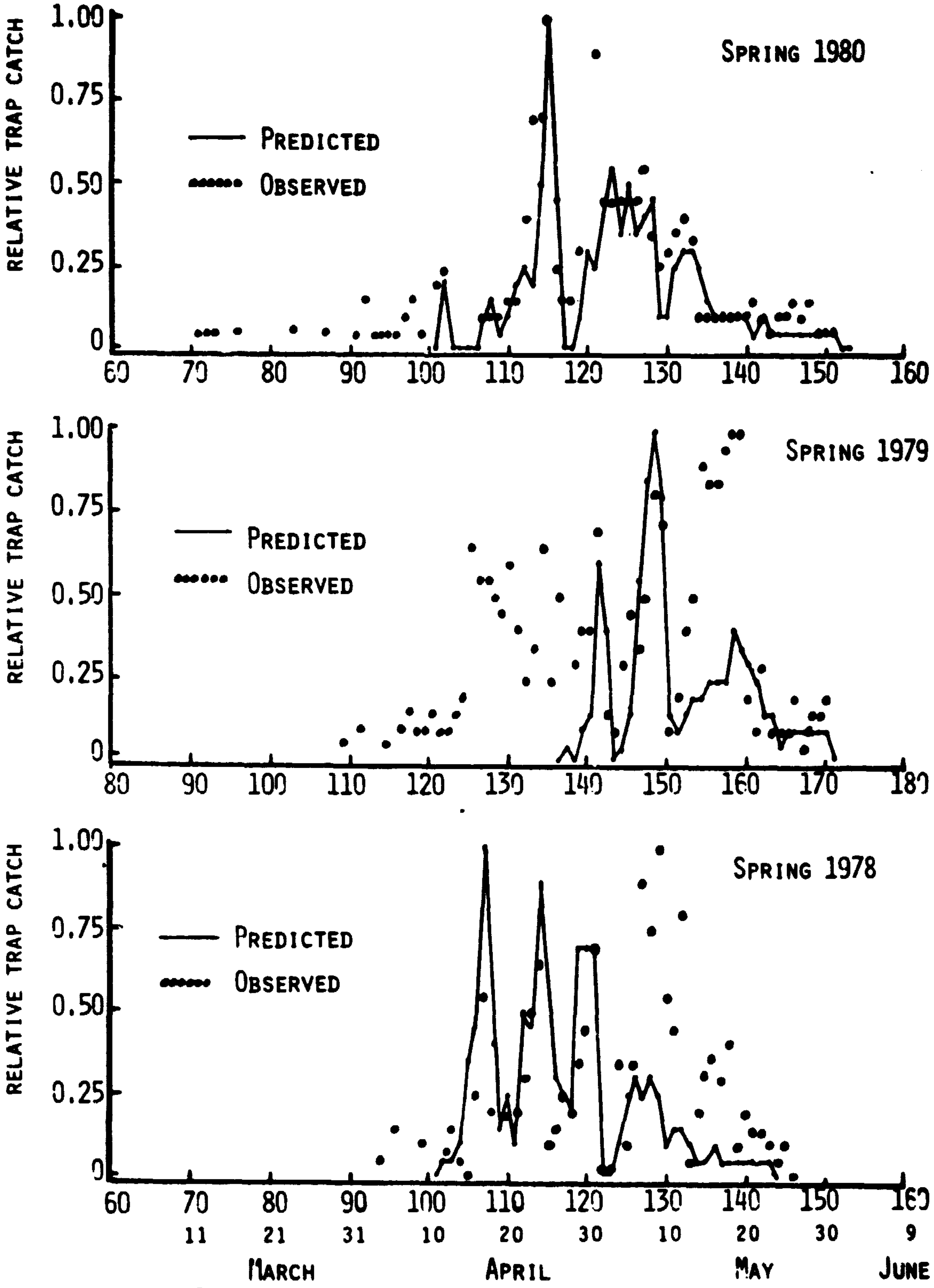

FIGURE 7A. OBSERVED PHEROMONE TRAP CATCHES OF MALES COMPARED TO PREDICTION BY MODEL. ALL DATA HAVE BEEN NORMALIZED.

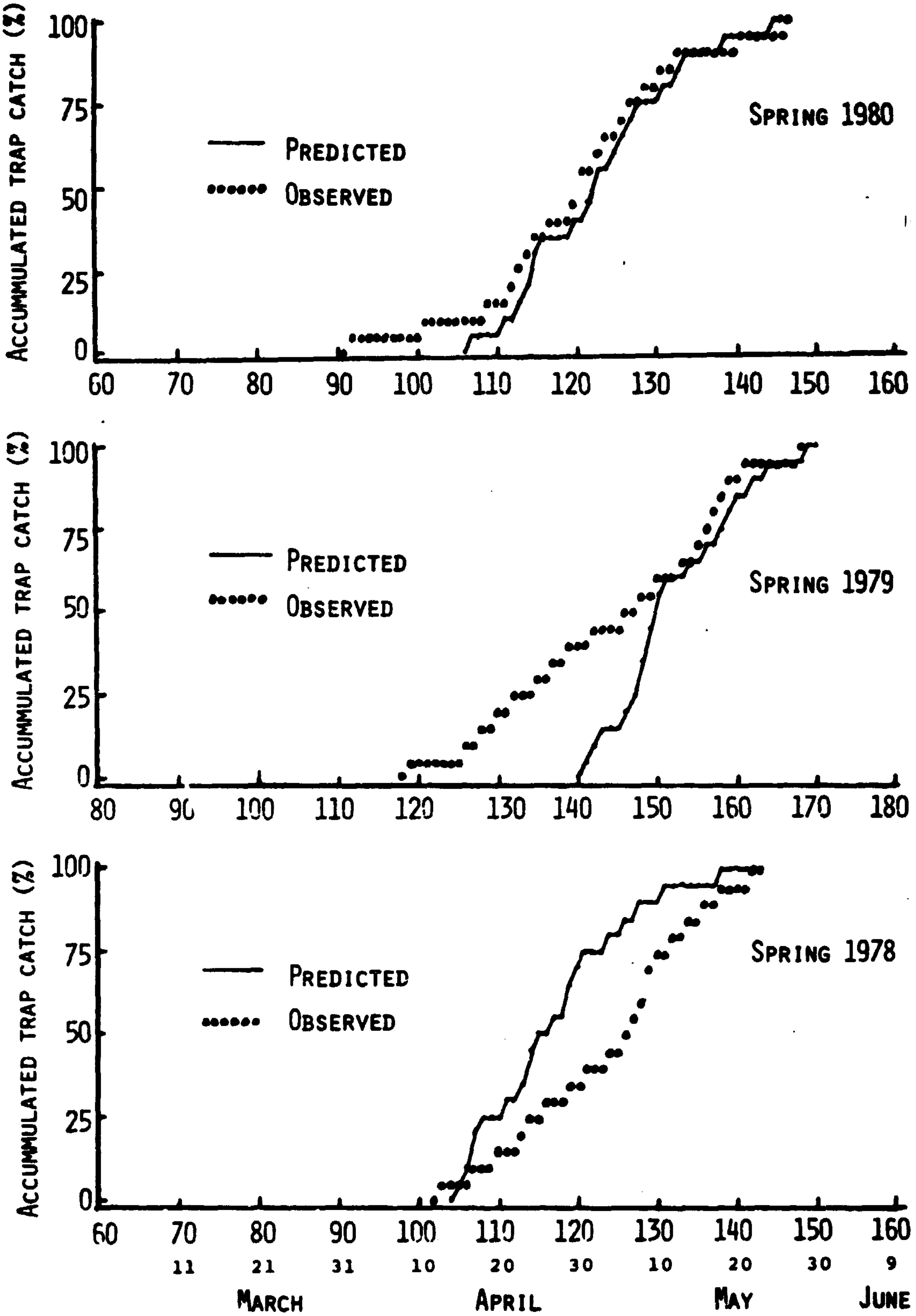

Figure 7b. Accummulated pheromone trap catch of males compared to prediction by model.

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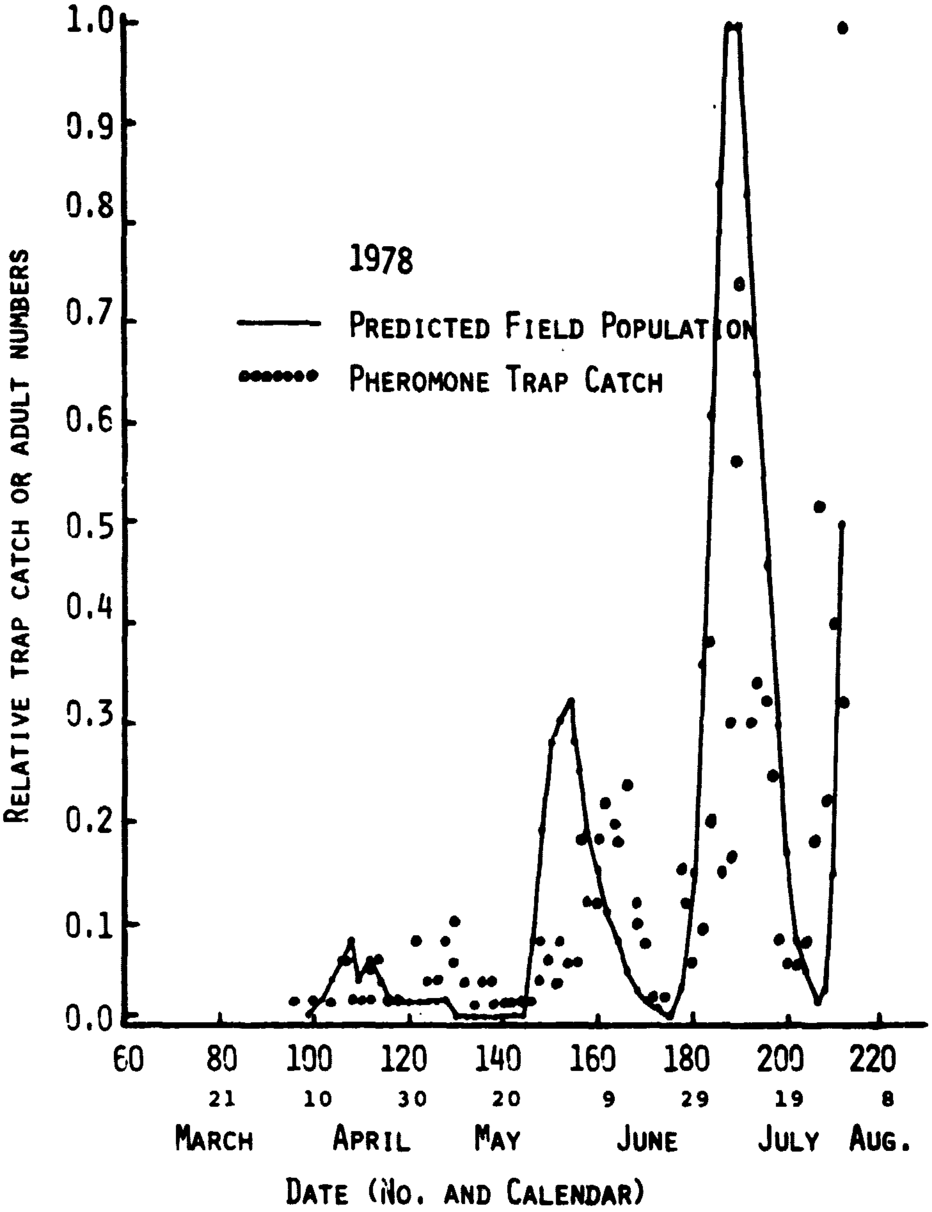

FIGURE 8. COMPARISON OF PHEROMONE TRAP CATCHES WITH PREDICTED ADULT NUMBERS BY MOTHZV. BOTH DATA WERE NORMALIZED.

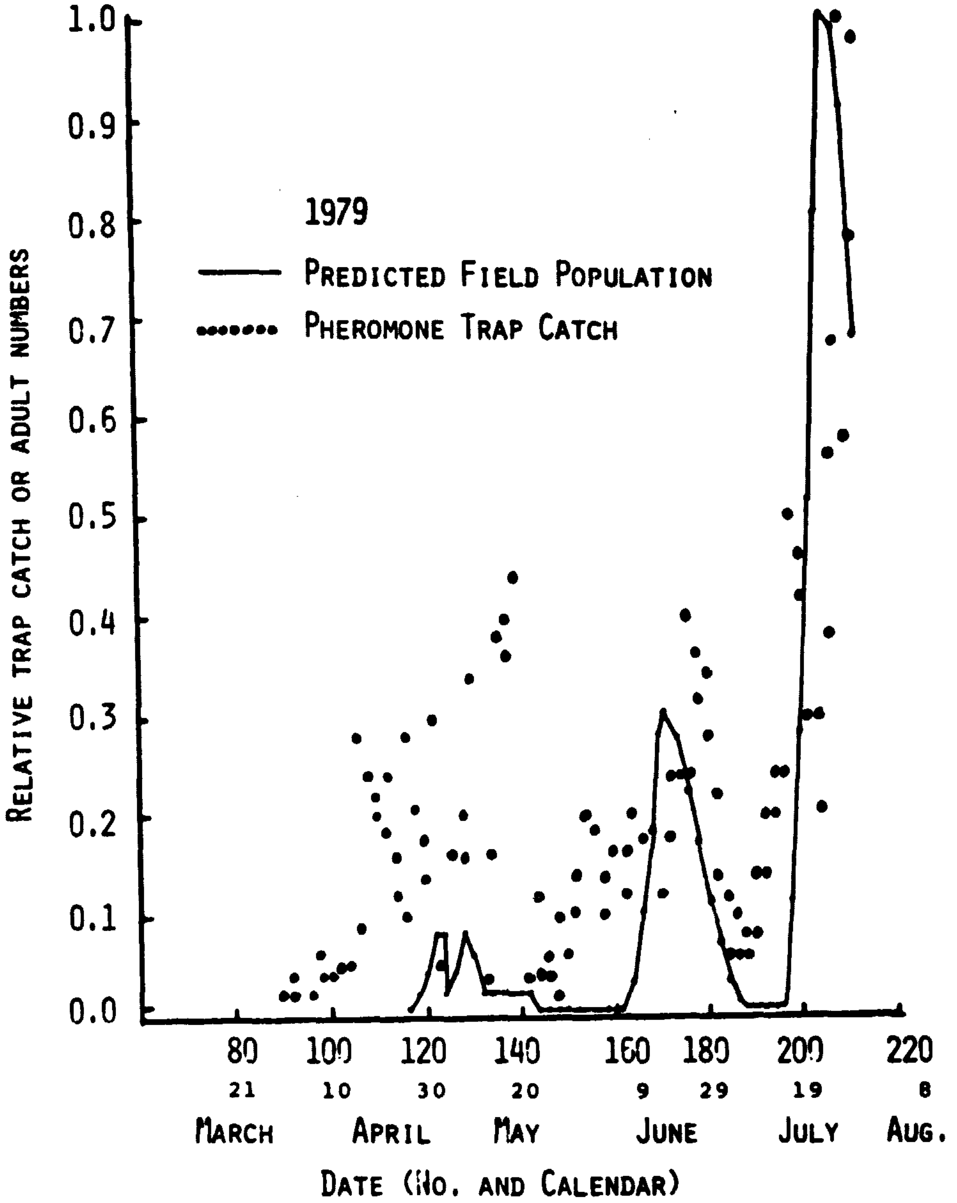

FIGURE 9. COMPARISON OF PHEROMONE TRAP CATCHES WITH PREDICTED ADULT NUMBERS BY MOTHZV. BOTH DATA WERE NORMALIZED.

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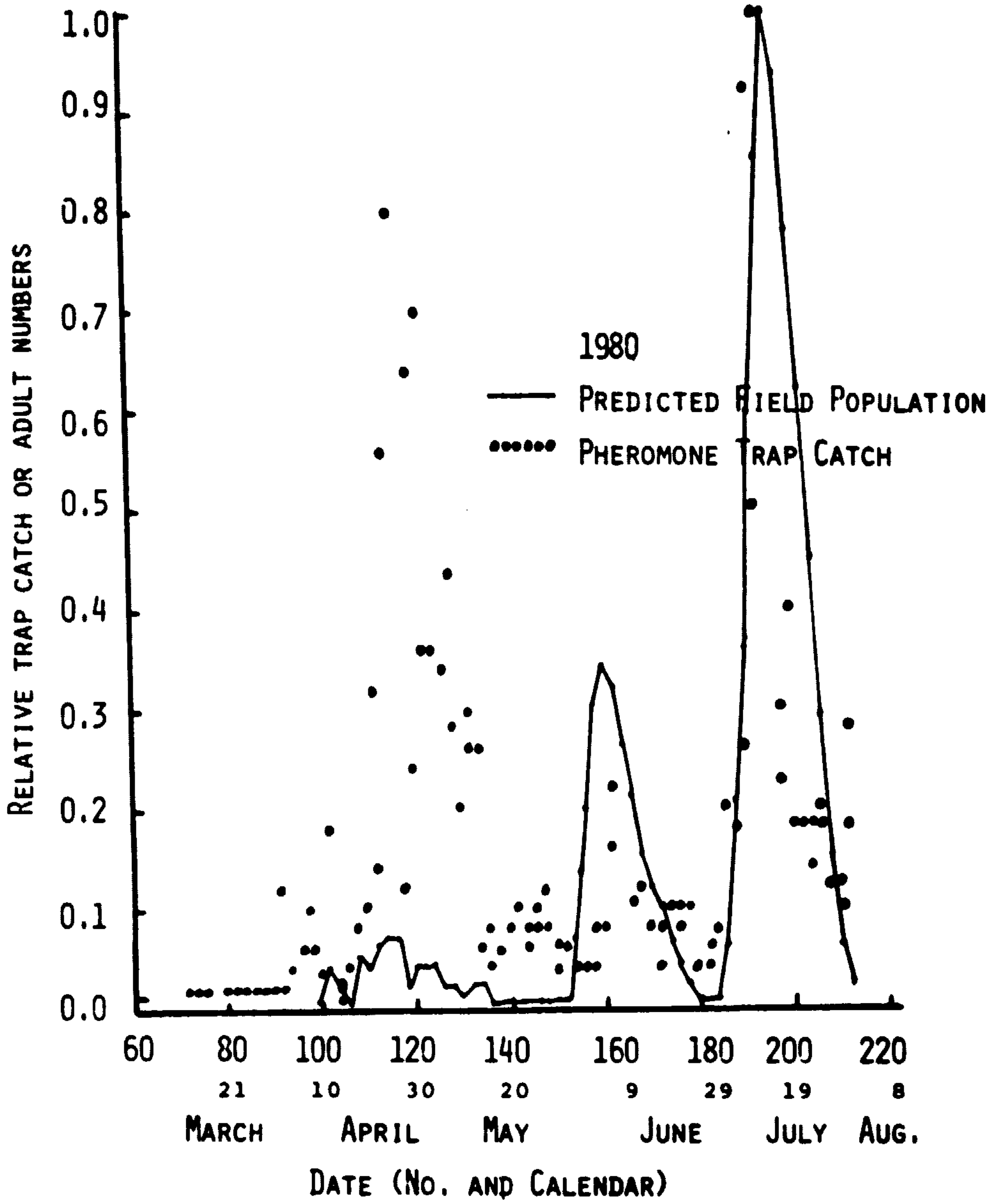

FIGURE 10. CAMPARISON OF PHEROMONE TRAP CATCHES WITH PREDICTED ADULT NUBMERS BY MOTHZV. BOTH DATA WERE NORMALIZED.