

### 3.3 Phenology and Seasonal Modeling in Insects<sup>1</sup>

William E. Bradshaw

*Biology Department  
University of Oregon  
Eugene, Oregon, 97403 USA*

#### 1 Introduction

Insects exhibit a wide variety of seasonal adaptations. Studies of seasonality in insects have generally considered whole populations rather than repeated observations of individuals. The reason for this approach is that insects, as a rule, are small, short-lived, and extremely abundant. Insects are therefore more cryptic, more ephemeral, and are potentially endowed with much greater genetic variability than most plants or vertebrates. The importance of these attributes in phenological studies cannot be overemphasized. In different seasons of the same year or during the same season of successive years, one can expect to find individuals and gene frequencies which are significantly different from those encountered in prior sample populations. Consequently, the insect phenologist may deal with greater variation in the timing of a phenophase or in the extent of population growth than a phenologist concerned with plants or vertebrates. Seasonal models of insect populations will reflect this greater variation by exhibiting greater variance or lower confidence limits in their prediction of future events than will models concerning plants or vertebrates.

#### 2 Definition of Insect Phenophases

The following phenophases are essentially reiterations or additions to those outlined by the US/IBP Phenology Committee (French *et al.*, 1972). Whenever possible, the terms have been left the same and only the definitions modified to correspond to insect bionomics.

<sup>1</sup> Research supported by the University of Oregon's Office of Scientific and Scholarly Research. Thanks to Philip Lounibos and Christina Holzapfel for their help with the manuscript.

---

KEYWORDS: Insect; phenophase; diapause; seasonality; phenology; modeling; latitudinal effects; pesticides control; photoperiodism; development.

- Arrival:** Emergence of dormant individuals or appearance of the stage of the life cycle following that in which dormancy occurs; arrival of migrants or seasonal immigrants.
- Departure:** Observation of dead or dormant individuals or noted absence of reliably observed individuals.
- Flocking:** Observation of swarms or aggregations.
- Molt:** Molting from one stage of development to the next: hatching from the egg, molting from one larval or nymphal instar to another, molting from larva to pupa, or molt from pupa or nymph to adult.
- Singing:** Characteristic song or call of the species.
- Courtship:** Ritual behavior or observation of mating pairs.
- Nesting:** Construction of characteristic structure by social or solitary insects; hoarding, construction of refugia.
- Eggs:** Appearance of eggs.
- Polymorphism:** Observation of a change in frequency of phenotypes; appearance of new phenotypes, including behavioral, morphological, physiological, or reproductive states.
- Voltinism:** Generations per year.

The first appearance of a given phenophase is often used to score its occurrence. The great variety of insects suggests that other portions or proportions of seasonal change will frequently be significant, and insect phenophases may have the following attributes:

- Onset:** First observation of a phenophase.
- Termination:** Last observation of a phenophase.
- Duration:** Time from onset to termination of a phenophase.
- Extent:** The number or proportion of organisms in a given phenophase.
- Timing:** When the onset, termination, maximum extent, or some other attribute of a phenophase occurs during the year.

### 3 Seasonal Arrival and Departure of Insects

Arrival and departure of insects at temperate latitudes are usually the consequence of terminating or initiating diapause. Diapause is a state of developmental dormancy brought about by inactivity of neuroendocrine centers in the brain; it persists until the brain again becomes endocrinologically active, even though conditions for development may be otherwise favorable (de Wilde, 1970). Diapause ordinarily endows an individual with resistance to environmental harshness and is known to occur at virtually any stage of development. Within a species or geographic race, diapause usually occurs only at a specific stage and thus synchronizes both the development of individuals within a population and development of that population with the seasonal cycle. Most of the discussion below concerning the factors controlling the onset and termination of diapause has been condensed from the excellent considerations of Danilevskii (1965), Andrewartha (1952), Lees (1955), and Beck (1968).

Obligate diapause is evoked endogenously without regard to the environment and imposes univoltinism upon an insect. More frequently, diapause is facultative and brought about by a variety of environmental parameters, including daylength, temperature, and food quality. Facultative diapause may occur in uni-, bi-, or multivoltine insects. At temperate latitudes, insects are mainly of the "long-day" variety, meaning that long days avert or terminate diapause and short days evoke or maintain it (Lees, 1955; Danilevskii, 1965). Nutritional food (Lees, 1955, pp. 37-39; Adkisson, 1961; Bull and Adkisson, 1962; Danilevskii, 1965, pp. 79-99) and high temperatures (Danilevskii, 1965; Beck, 1968) complement the action of long-day photoperiod. Among long-day insects, diapause is usually determined in phenophases proximal to that in which diapause occurs.

Short-day insects are those in which short days avert or terminate diapause and long days promote or maintain it. Short-day insects tend to occur at southern latitudes where summer dryness and not winter cold represents the major threat to insect survival (Geyspits, 1953; Masaki, 1958). Therefore it is not surprising that among short-day species, warm temperatures complement the action of short-day rather than long-day photoperiod. At more northern latitudes, short-day evocation of diapause may occur when diapause is determined during a phenophase remote from that in which diapause takes place (Kogure, 1933).

The resumption of development among diapausing individuals involves two distinct processes: the termination of diapause, *per se*, which renders the insect competent to develop, and postdiapause morphogenesis. The distinction is extremely important for modeling seasonality since the duration of these periods varies with respect to the two predominant factors mediating the termination of diapause: temperature and photoperiod. The termination of diapause in many insects is brought about by simple chilling at temperatures well below those required for normal morphogenesis (Andrewartha, 1952; Lees, 1955, pp. 53-64). The termination of diapause may also be brought about entirely through the action of photoperiod (Beck, 1968, pp. 151-161; Bradshaw and Lounibos, 1972). The action of photoperiod is generally more pronounced at temperatures compatible with morphogenesis than at lower temperatures (Danilevskii, 1965, pp. 106-113). Once diapause is terminated, postdiapause morphogenesis continues regardless of photoperiod and is affected by the same factors that control continuous development.

#### 4 Modeling Seasonality in Insects

Modeling of seasonality in insects has two major components: modeling arrival and departure and modeling the continuous morphological, behavioral, or physiological phenophases which occur in between. Development during favorable conditions is controlled largely by food, temperature, and humidity. Presence and availability of food in nature are difficult to quantify, but reasonable knowledge of an insect's bionomics may justify assumptions concerning correlations between climate and food availability. Davidson and Andrewartha (1948), using multiple regression analysis, were able to predict the numbers of rose-thrips likely to be

present during spring and early summer, based on four sets of meteorological measurements which accounted for 76% of the interannual variability among the population. Of these parameters, they found temperature during the preceding autumn to be the most highly correlated with changes in population density. They proposed that this strong effect of autumnal temperature was due to greater growth, earlier maturation, and earlier pollen production (= thrip food) by the host plant. The important point is that they did not have to quantify food availability to make their predictions of population size. A reasonable level of observation and assumptions sufficed.

Both temperature and humidity vary widely in space and time among insect microhabitats (Chauvin, 1967, pp. 15-51). Like low temperature, low humidity tends to retard development, primarily among insects that normally live in otherwise humid habitats (Bursell, 1964). Insects are often adept at seeking out favorable microhabitats (Fraenkel and Gunn, 1961), and the availability of favorable microclimates probably correlates well with sunlight, rainfall, temperature, and evaporative index. Haufe and Burgess (1956) sought to make such a correlation. They considered tundra and taiga pools inhabited by mosquito larvae. They found that pool surface temperature ( $X$ ) was related to air temperature ( $T$ ), hours of sunshine ( $Y$ ), and wind-chill or dry-cooling power of the atmosphere ( $Z$ ):

$$X = a \left[ \frac{\sqrt{Y \times 1} \left( \frac{T_1 \times T_2}{2} \right)}{Z} \right]^b \quad (1)$$

where  $a$  and  $b$  are constants,  $T_1$  the maximum daily temperature ( $^{\circ}\text{F}$ ) minus 32, and  $T_2$  the minimum daily temperature ( $^{\circ}\text{F}$ ) minus 32. Haufe and Burgess (1956) observed that the mosquito larvae in these pools tended to have species-specific temperature preferences. They would stay at shallow, warm depths until the temperature exceeded their preferred level and then migrate downward. Therefore, whenever the surface temperature exceeded their preferred level, the effective temperature was set equal to the preferred temperature.

Once one is able to correlate standard meteorological data with insect microclimates, a variety of equations exist which relate rate of development to temperature. Each equation, in a sense, represents a different model relating the duration of a phenophase to temperature. The most commonly used equation is the thermal summation formula:

$$D = \frac{b}{T - a} \quad (2)$$

where  $D$  is the duration of the phenophase,  $T$  is the temperature, and  $a$  and  $b$  are constants. The constant  $a$  is the threshold temperature below which development ceases or the developmental zero. The constant  $b$  is the thermal constant and is the number of degree-days above developmental zero required for completion of a given phenophase. Temperature data below  $a$  must be set equal to  $a$  since regressive development does not ordinarily occur.

Danilevskii (1965, pp. 223–234) found that in the cabbage moth, *Barathra brassicae*, the developmental zero was around 10°C and the thermal constant about 560–580 degree-days. As shown in Fig. 1, *B. brassicae* is univoltine near Leningrad (620 degree-days), bivoltine near Veronezh (1100 degree-days) and trivoltine in eastern Georgia (1860 degree-days). Facultative pupal diapause in all strains of *B. brassicae* is mediated by photoperiod. The critical photoperiod at a given temperature increases with latitude of origin but critical photoperiod is lowered by higher temperatures and raised by lower ones. Thus, near Leningrad, summer temperatures do not normally rise above 18°C; consequently, all larvae experience short days and result in diapausing pupae. Near Veronezh, warmer temperatures and lower critical photoperiod combine to produce long-day conditions from about May 30 to July 15. The first generation then results in developing pupae and the

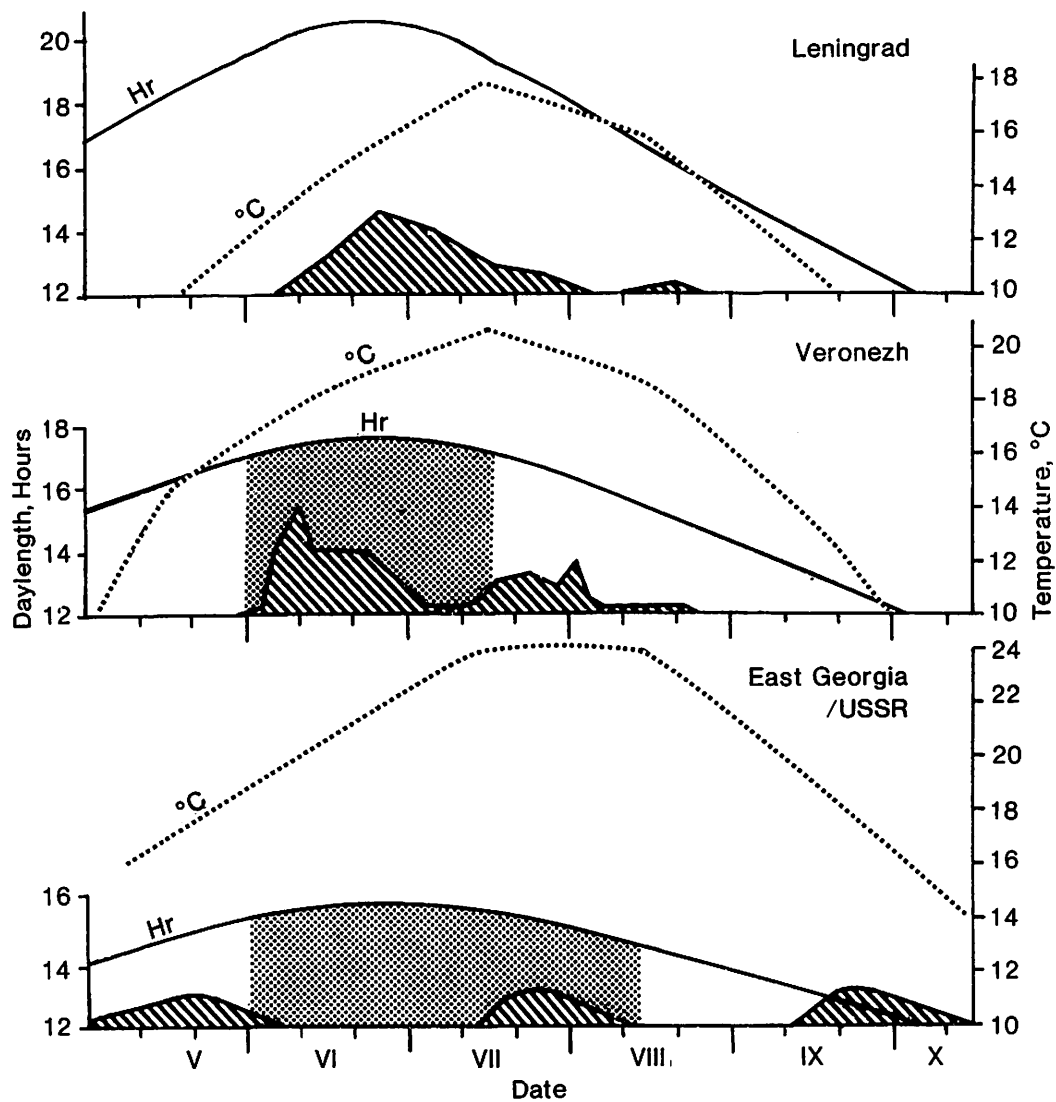


Fig. 1. Seasonal pattern in development of *Barathra brassicae* from Leningrad (60° N lat.), Veronezh (52° N lat.), and eastern Georgia (USSR) (42° N lat.). Diagonal shading: relative number of flying adults; light shading: diapause averting photoperiod. (After Danilevskii, 1965.)

second in diapausing pupae. In eastern Georgia, long-day conditions are present from about May 30 to August 15. The earliest larvae see short days; consequently, 22 to 30% of the first summer generation enters diapause. The latest larvae of the second summer generation likewise see short days and 45 to 60% of this generation enter diapause. All of the larvae of the third generation enter diapause. Some of the diapausing pupae of the first summer generation do not overwinter but emerge in the fall at about the same time as the third generation (Dolidze, 1957). This response in eastern Georgia corresponds well with that observed by Masaki (1956) in Japan at the same latitude where *B. brassicae* commences an aestival as well as an hibernal diapause. At still lower latitudes in Japan, the aestival diapause predominates. The very important point here is that a seasonal model based upon physiological experiments in the laboratory and using average temperature in the field for input data is likely to provide a good prediction of voltinism and departure under natural conditions.

Summation of degree-days does not always provide a satisfactory model for the relation between temperature and the completion of a phenophase. Other formulas based on various exponential, logistic, and catenary functions are provided by Wigglesworth (1965), Huffaker (1944), Clements (1963), and Nielsen and Evans (1960). These formulations are all based on uniform environmental temperatures, a condition which hardly ever exists in nature. Headlee (1940, 1941) has found that fluctuating temperatures may have a different effect than a constant temperature equal to the arithmetic mean of the fluctuating temperature. Cloudsley-Thomson (1953) has, however, pointed out that the arithmetic mean would be appropriate only when temperature has a linear relationship to biological rate processes, as in Equation (2). Otherwise, temperatures have to be weighted according to their nonlinear properties before summation. Thus logarithmic or other transforms of temperature data may yield more significant correlations between environmental temperature and predictability of phenophases.

Good models predicting arrival are equally as important as those describing departure. Arrival serves as the starting point of the phenological year and is largely responsible for the timing of the ensuing phenophases. Late arrival may delay the phenophases which are responsive to photoperiod so that an ordinarily bivoltine organism becomes univoltine (Danilevskii, 1965, pp. 212-221). Similarly, early arrival may result in a second generation with many nondiapausing individuals which are eliminated by winter. The timing of arrival in a given year can therefore affect the extent of population growth not only in that year, but in the subsequent one as well.

Individuals among a population may be in a variety of developmental stages when the transition from diapause-averting to diapause-promoting conditions occur. Departure at the end of the phenological year may therefore be gradual. By marked contrast, when the transition from diapause-maintaining to diapause-terminating conditions occur, individuals of a population tend to be in a uniform stage of development. Arrival can therefore be extremely abrupt, resulting in the sudden appearance of large numbers of insects. This difference in arrival and departure is illustrated by *Chaoborus crystallinus* whose larvae live in shallow paleartic ponds and diapause in the fourth larval instar beneath the winter ice

(Parma, 1969) (Fig. 2). The autumnal rise in proportion of fourth instar larvae shows that the onset of diapause takes place over a two-month period; vernal decline in the proportion of fourth instar larvae indicates the rapid, synchronous termination of diapause. Adult emergence in *Chaoborus* can also be synchronized through the action of, and not despite, fluctuating temperatures. Larvae of *C. americanus* live in shallow nearctic ponds. Diapause occurs in the fourth larval instar and is terminated through the action of feeding and long-day photoperiod (Bradshaw, 1969). Postdiapause morphogenesis then leads to pupation and finally adult emergence. Each of these three phenophases—termination of diapause, post-diapause morphogenesis, and the duration of the pupal stage—has its own relation

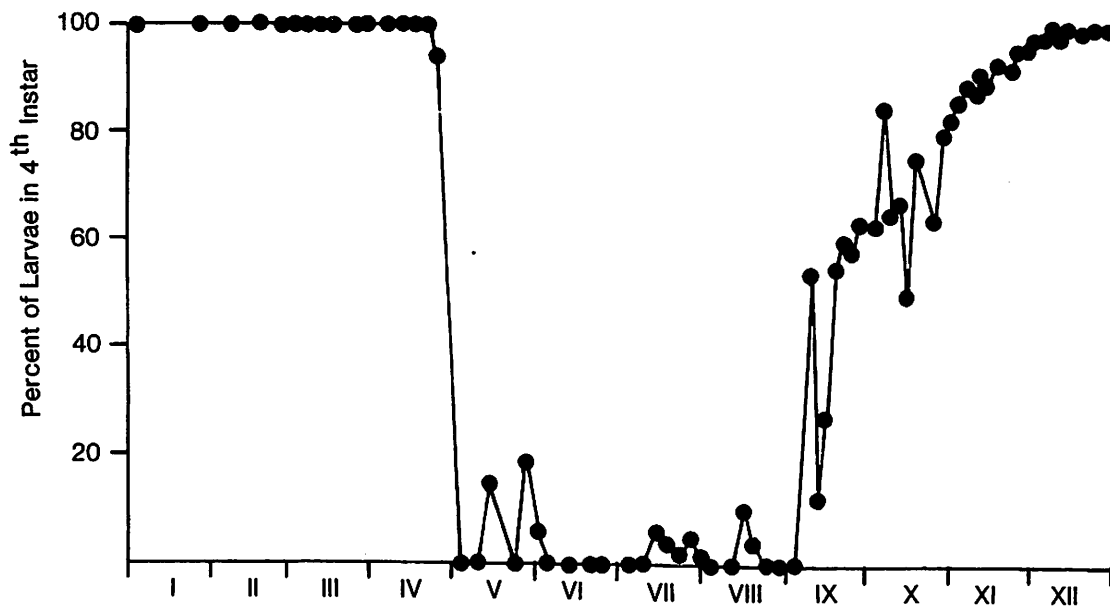


Fig. 2. Seasonal variation in the proportion of fourth instar larvae of *Chaoborus crystallinus*. (After Parma, 1969.)

to temperature as shown by the equations in Fig. 3. These equations serve as models of how each of these phenophases would progress during the spring. Cumulative percent completion of a phenophase can then be calculated as:

$$(\% \text{ completion})_t = (\% \text{ completion})_{t-1} + \frac{100}{\text{duration of phenophase at } T^\circ\text{C}} \quad (3)$$

where  $t$  is the present day,  $t-1$  the preceding day, and  $T^\circ\text{C}$  the average temperature on calendar day  $t$ . If temperatures were constant, one would expect that larvae commencing the termination of diapause 20 days apart would emerge as adults over a 20-day period. But it can be seen from Fig. 3 that under conditions of fluctuating temperature, adults emerge within a four-day period.

The most important aspect in determining the arrival of *C. americanus* adults in the above example is the termination of diapause. In the majority of insects, the termination of diapause is controlled mainly by temperature or photoperiod. These factors are considered below.

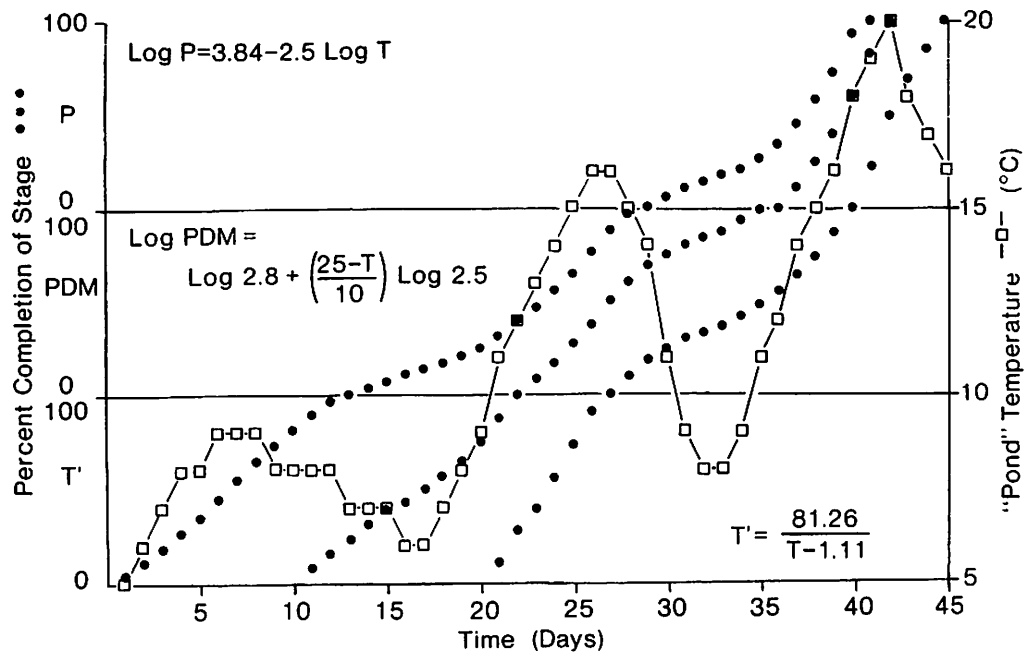


Fig. 3. Development of *Chaoborus americanus* in a fluctuating thermal environment. The duration of diapause termination ( $T'$ ), postdiapause morphogenesis ( $PDM$ ), and the pupal stage ( $P$ ) are expressed as a function of temperature ( $T$ ). Pond temperature was determined by drawing a smooth curve through temperature data from a shallow pond in southern Michigan during the spring of 1969. Three populations were presumed to initiate the termination of diapause on days 0, 10, and 20; they emerged as adults on days 40, 42, and 45, respectively (After Bradshaw, 1973).

The optimum chilling temperature for diapause termination may lie within the normal range of environmental temperatures and may be well above the lower sublethal limit (Lees, 1955, pp. 50–67; Danilevskii, 1965, pp. 1–35; Andrewartha, 1952). A plot of diapause duration as a function of temperature is therefore usually U-shaped; parabolic, elliptical, or hyperbolic functions can often be fitted to experimental data to form a model. Such a plot is frequently asymmetric about the temperature optimum, and two formulations are then required for a model: one equation for temperatures above the optimum and one for temperatures below it.

Problems concerning photoperiodically terminated diapause are various. Critical photoperiods as defined in the laboratory may be a physiologically useful index of photoperiodic response, but have several drawbacks for seasonal models: (1) In the laboratory, one usually employs instantaneous dawns and dusks, quite unlike the natural sequence of twilight. (2) There is a certain amount of reciprocity between the critical daylength and the duration of the experiment (Paris and Jenner, 1959). (3) Daylengths in nature are not static, but change with the season. (4) On a given date after the vernal equinox, daylengths are longer in the north than in the south. That insects from northern latitudes have longer critical daylengths than those from southern latitudes (Danilevskii, 1965; Beck, 1968) does not necessarily imply that the former will commence development at a later calendar date than the latter.

To account for some of these problems, I have proposed a model which predicts



development of a photoperiodic mosquito in constant-temperature years with instantaneous dawns and dusks but changing photophases (Bradshaw, 1971). The mosquito *Wyeomyia smithii* is a long-day insect which diapauses in the third larval instar. The resumption of development is scored by molting to the fourth instar; the number of days required for half the population to molt is designated as  $IV_{50}$  (Bradshaw and Lounibos, 1972).  $IV_{50}$  is a function of daylength, being longest at the critical photoperiod, declining rapidly at longer daylengths, and finally reaching a minimum value at a daylength approximately 1 hr longer than the critical photoperiod. The crucial point is that, instead of asking how much development is evoked by a given daylength, one is asking how long does it take an animal to develop in response to a given photoperiod.  $IV_{50}$  as a function of several static daylengths is first determined experimentally, and date of median molting during dynamic daylengths predicted from the following model (Equations 4 to 9) [where  $t$  = day of solar year,  $t-1$  = day before  $t$ , and  $(IV_{50})_t = IV_{50}$  elicited by a static daylength equal to the hours of light per day on day  $t$ ]:

- A. Commence with  $t$  whose daylength elicits the maximum  $IV_{50}$  (4)
- B.  $t = t \times 1$  (i.e., add 1 day to  $t$ ) (5)
- C. (projected date) $_t = t + IV_{50}$  (6)
- D. If (projected date) $_t$  earlier than (projected date) $_{t-1}$ , go to B (7)
- D'. If (projected date) $_t$  later than or equal to (projected date) $_{t-1}$ , go to E (8)
- E. Predicted date of median molting = (projected date) $_{t-1}$  (9)

For an artificial year created by an astronomic time clock at 25°C, the model successfully predicted median molting to within four days. Instead of an astronomic time clock, tables of sunrise, sunset, and twilight could be used and calendar dates of median molting in a constant-temperature year could be predicted. These calendar dates would be independent of the duration of the original static photoperiod experiments. Furthermore, they can be based on whatever astronomic time units (extent of twilight) are subsequently found to be important. Finally, the model can be used to estimate the extent to which longer critical daylengths at higher latitudes are due to real differences in environmental timing of development and to which extent they are due to the simple consequences of higher latitude.

The format employed in the model is intended to be compatible with computer programming. Continuous functions, while creating elegant models, do not always conform to the vagaries of insect physiology and climatic change. In such cases, the iterative capabilities of digital computers can be used to sum the effects of climatic variation on the progress of a phenophase, be it one controlling arrival, departure, or the duration of any phenophase in between.

## 5 Prospects

Levins (1969) and Cohen (1970) have formulated general models for the optimal timing of diapause. Both models require probabilities of survivorship as their input data, data which are at best difficult to obtain. An alternative approach has been

pursued by Danilevskii (1965), who assumed that populations have already optimized the timing of diapause and that their seasonal development may be explained on the basis of known physiological rate processes. Danilevskii (1965) did not formulate a general model but it is clear from his work that seasonal development in insects may reliably be predicted from quantitative meteorological measurements if one knows the aspects of the environment that affect developmental rate processes. Models of photoperiodic reactions (Equations 4 to 9), when combined with those analyzing the temperature dependence of individual phenophases (Fig. 3), will eventually result in predictive models of vernal development. Models describing the timing and extent of successive phenophases during the ensuing periods of continuous development will likely evolve from multiple regression analyses of meteorological data similar to those of Davidson and Andrewartha (1948) and Haute and Burgess (1956).

Accurate predictions of seasonality would permit the use of nonpersistent pesticides without requiring multiple application. Models predicting arrival and departure would indicate how many generations could be expected in a given year, and whether organisms found late in the season would be destined to diapause or whether they would continue developing and perish in winter without any intervention by man. Finally, if a model predicts a small outbreak of a pest species in a given year, long-term interests may be better served by not taking any control measures and permitting the pest species to maintain a healthy population of natural predators and parasites. The future of seasonal models in insects must therefore coordinate studies of insect physiology, biometeorology, and experimental population biology.

## References

- Adkisson, P. L. 1961. Effect of larval diet on the seasonal occurrence of diapause in the pink bollworm. *J. Econ. Entomol.* 54, 1107-1112.
- Andrewartha, H. G. 1952. Diapause in relation to the ecology of insects. *Biol. Rev.* 27, 50-107.
- Beck, S. D. 1968. *Insect Photoperiodism*. New York-London: Academic Press.
- Bradshaw, W. E. 1969. Major environmental factors inducing the termination of larval diapause in *Chaoborus americanus* Johansen (Diptera: Culicidae). *Biol. Bull.* 136, 2-8.
- 1971. Photoperiodic timing of development in the pitcher-plant mosquito, *Wyeomyia smithii*. *Amer. Zool.* 11, 670-671.
- 1973. Homeostasis and polymorphism in vernal development of *Chaoborus americanus*. *Ecology*, 54, 1247-1259.
- , and L. P. Lounibos. 1972. Photoperiodic control of development in the pitcher-plant mosquito, *Wyeomyia smithii*. *Can. J. Zool.* 50, 713-719.
- Bull, D. L., and P. L. Adkisson. 1962. Fat content of the larval diet as a factor influencing diapause and growth rate of the pink bollworm. *Ann. Entomol. Soc. Am.* 55, 499-502.
- Bursell, E. 1964. Environmental aspects: Humidity. In *The Physiology of the Insecta*, M. Rockstein, Ed. Vol. 1, pp. 323-361. New York-London: Academic Press.
- Chauvin, R. 1967. *The World of an Insect*. pp. 15-51. New York: McGraw-Hill.
- Clements, A. N. 1963. *The Physiology of Mosquitoes*. pp. 74-79. New York: Macmillan.

- Cloudsley-Thomson, J. L. 1953. The significance of fluctuating temperatures on the physiology and ecology of insects. *Entomologist* 86, 183-189.
- Cohen, D. 1970. A theoretical model for the optimal timing of diapause. *Am. Nat.* 104, 389-400.
- Danilevskii, A. S. 1965. *Photoperiodism and Seasonal Development of Insects*. Edinburgh and London: Oliver and Boyd.
- Davidson, J., and H. G. Andrewartha. 1948. The influence of rainfall, evaporation, and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *J. Anim. Ecol.* 17, 200-222.
- Dolidze, G. V. 1957. Study of cabbage-head insect pests in eastern Georgia. *Trans. Acad. Sci. Georgia SSR* 18, 83-90.
- Fraenkel, G. S., and D. L. Gunn. 1961. *The Orientation of Animals: Kineses, Taxes, and Compass Reactions*. New York: Dover.
- French, N. R., C. H. Lamoureux, H. Lieth, J. A. MacMahon, W. A. McKee, D. Parsons, F. Stearns, P. Webber, and D. Zobel. 1972. *Report of the US/IBP Phenology Committee*. Environmental Programs Coordinating Office, U.S. Component of the International Biological Program.
- Geyspits, K. F. 1953. The reaction of univoltine Lepidoptera to day-length. *Entomol. Rev.* 33, 17-31.
- Haufe, W. O., and L. Burgess. Development of *Aedes* (Diptera: Culicidae) at Fort Churchill, Manitoba, and prediction of dates of emergence. *Ecology* 37, 500-519.
- Headlee, T. J. 1940. The relative effects on insect metabolism of temperatures derived from constant and variable sources. *J. Econ. Entomol.* 33, 361-364.
- 1941. Further studies on the relative effects on insect metabolism of temperatures derived from constant and variable sources. *J. Econ. Entomol.* 34, 171-174.
- Huffaker, C. B. 1944. The temperature relations of the immature stages of the malarial mosquito *Anopheles quadrimaculatus* Say, with a comparison of the developmental power of constant and variable temperatures in insect metabolism. *Ann. Entomol. Soc. Am.* 37, 1-27.
- Kogure, M. 1933. The influence of light and temperature on certain characters of the silkworm, *Bombyx mori*. *J. Dept. Agr. Kyushu Univ.* 4, 1-93.
- Lees, A. D. 1955. *The Physiology of Diapause in Arthropods*. London and New York: Cambridge University Press.
- Levins, R. 1969. Dormancy as an adaptive strategy. *Symp. Soc. Exp. Biol.* 23, 1-10.
- Masaki, S. 1956. The effect of temperature on the termination of pupal diapause in *Barathra brassicae* L. *Japan. J. Appl. Zool.* 21 (3), 97-107.
- 1958. The response of a "short-day" insect to certain external factors: The induction of diapause in *Abraxis miranda* Butl. *Japan. J. Appl. Entomol. Zool.* 2, 4, 285-294.
- Nielsen, E. T., and D. G. Evans. 1960. Duration of the pupal stage of *Aedes taeniorhynchus* with a discussion of the velocity of development as a function of temperature. *Oikos* 11, 200-221.
- Paris, O. H., and C. E. Jenner. 1958. Photoperiodic control of diapause in the pitcher-plant midge, *Metricnemus knabi*. In *Photoperiodism and Related Phenomena in Plants and Animals*, R. B. Withrow, ed. pp. 601-624. Washington D.C.: American Association for the Advancement of Science.
- Parma, S. 1969. The life cycle of *Chaoborus crystallinus* (DeGeer) (Diptera, Chaoboridae) in a Dutch pond. *Verh. Internat. Verein. Limnol.* 17, 888-894.
- Wigglesworth, V. B. 1965. *Insect Physiology*. pp. 594-628. London: Methuen.
- de Wilde, J. 1970. Hormones and insect diapause. In *Hormones and the Environment*, G. K. Benson and J. G. Philipps, eds. Cambridge: University Press.