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Estimation of Cumulative Change of State with the Weibull Function

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Insects often respond to experimental treatment with an irreversible change in condition. For example, insects exposed to a toxicant may die, or insects in one stage of development may attain the next stage. When nondisruptive observations over time can be made on the same group of individuals, definition of the time trend in the proportion that changed state may enhance the description of the treatment response and facilitate comparisons among treatments. In some experiments, the time trend may be the criterion for choosing one treatment in preference to another.

We describe here the use of the three-parameter Weibull function to depict the unimodal frequency distribution of state with time. Examples of two types of entomological experiments in which this statistical method is applicable are presented, with a description of situations to which the Weibull function is not well suited. Use of the Weibull function in ecological studies of survivorship has previously been described by Pinder et al. (1978).

General Background

The cumulative proportion of test subjects that have changed state by a given time may be denoted as F(x), where x is a specific time. The graph of function F(x) over x is assumed to define a smooth, S-shaped curve. This monotonic trend, in itself, specifies that the change of state is irreversible; the smoothness suggests that the trend in the proportion represents responses of a large number of subjects. The time of change of state is the random variable in the cumulative distribution function (CDF).

For example, Fig. 1A shows the cumulative mortality patterns for two insecticide treatments. For times (h), both curves are similar until about 7 h. By 12 h, the two trends are markedly different, but by 25 h both treatments have resulted in total mortality. Obviously, had observations been restricted to a single time, such as 12 h, conclusions about relative effectiveness would differ greatly from those based on a later time, such as 25 h.

Changes of different magnitude may occur in each F(x) during different time intervals. For example, many changes occurred during the 8th hour after application of treatment I (Fig. 1A), but few occurred during the 13th hour. The function f(x) describes the instantaneous change occurring at time x (Fig. 1B). For each treatment, f(x) is assumed to be a single, modal distribution. In Fig. 1B, treatment I shows a maximum instantaneous rate at about 9 h and a slight tail to the left; treatment II has an elongated tail to the right and a maximum rate of change at about 8 h.

The Weibull Model

The Weibull distribution, a function used in materials reliability testing, can describe a continuous unimodal distribution of time to change of state while allowing skewness in either direction. This function has three parameters denoted as location (a), scale (b), and shape (c). With the Weibull function, the equation for the cumulative distribution is:

$$F(x) = 1 - \exp\{-[(x - a)/b]^{-c}\}, \quad \text{for } x \geq a \geq 0 \qquad (1)$$

In general, $b > 0$ and $c > 0$. This equation may be solved directly with a pocket calculator with a logarithmic function. The location parameter a is the earliest time beyond which the probability of a change of state rises above zero. If the time x is given as $a+b$, then $F(x) \sim 0.63$, i.e., about 63% of the changes will occur by the time $a+b$.

The probability density, or instantaneous change in the CDF, for the Weibull function is:

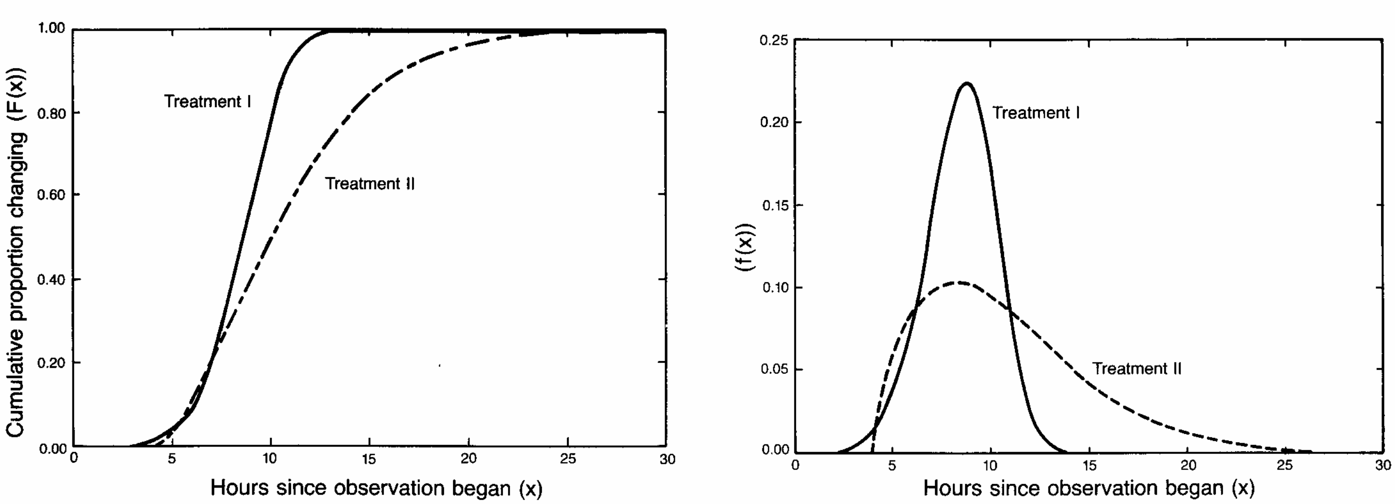

Fig. 1. (A) Time trends in response resulting from two different hypothetical treatments; (B) instantaneous change functions for the time trends.

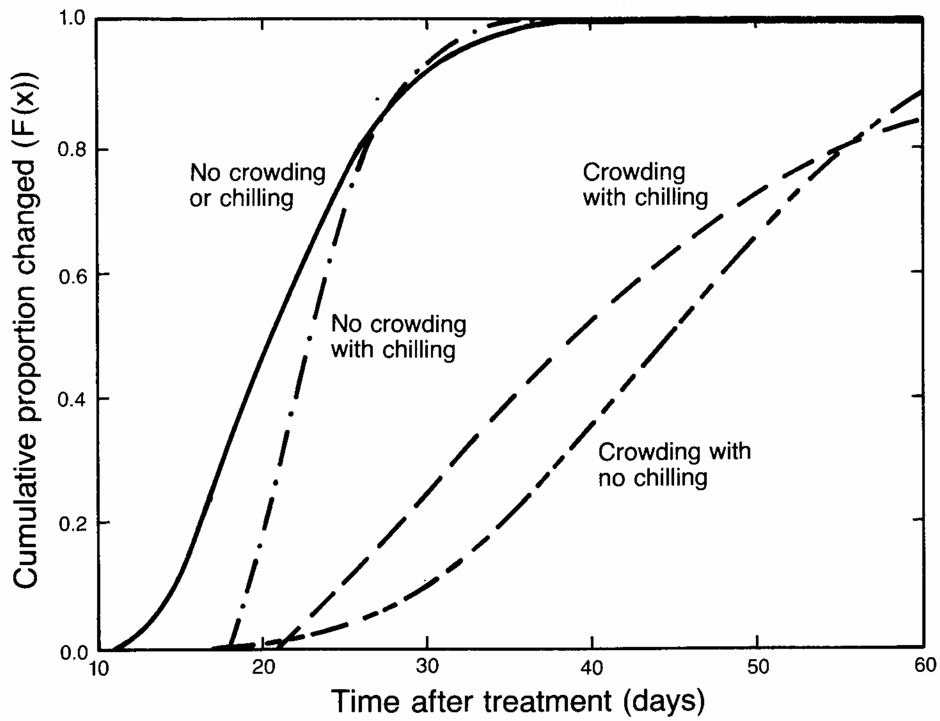

Fig. 2. Time trends in larval-pupal ecdysis after four treatments of *G. mellonella.*

$$f(x) = (c/b)\,[(x - a)/b]^{c-1} \exp\{-[(x - a)/b]^c\} \qquad (2)$$

When $c = 3.25$ to 3.61, f(x) approximates the normal distribution. Below 3.25, a progressively more pronounced tail to the right appears (positive skewness); above 3.61, progressively more negative skewness is observed.

Other useful statistics can be calculated. If equation 1 is rearranged to a specific proportion (p) and solved for the associated time (x_p), percentiles are determined as:

$$xp = a + b\,[-\ln(1 - p)]^{\frac{1}{c}} \qquad (3)$$

For example, the time to 50% mortality in treatment 1 (Fig. 1A) is 8.5 h where $a = 0$, $b = 9.12$, and $c = 5.48$. The mode, or time at which maximum rate of change occurs is, for $c \geq 1$.

$$\text{mode} = a + b\left[1 - \frac{1}{c}\right]^{\frac{1}{c}} \qquad (4)$$

Two other statistics, the mean (equation 5) and the variance (equation 6), involve the gamma (Γ) function and are usually calculated with a computer.

$$\text{mean} = a + b\Gamma_1 \qquad (5)$$

$$\text{variance} = b^2\,[\Gamma_2 - \Gamma_1^2] \qquad (6)$$

where

$$\Gamma_k = \Gamma\left(1 - \frac{k}{c}\right)$$

with values of the gamma function defined as $\Gamma_{(z)} = {}_0\!\int^{\infty} t^{z-1}\, e^{-t} dt$.

Parameter Estimation

Quantifying the time trend for changes of state requires that nondisruptive observations be made frequently enough to establish a reasonably precise determination of the time when each test subject changed state. This does not mean, however, that the experiment must be continued until all test subjects have changed. The experiment may be terminated and the number of unchanged subjects recorded in instances where the additional information does not justify continuation until all test subjects have changed. Appropriate procedures for Weibull parameter estimation have been developed for such censored samples. Some of these procedures have been implemented in a computer program.[1] Provisions are included in this program to reject the parameter estimation assignment when data are inadequate, as may occur when observations are not made frequently enough, the time trend is not unimodal, or an experiment is terminated too early.

Sample Applications

Time Trends in Metamorphosis

The application of the Weibull function can be illustrated by two series of experiments. In one series, last-instar greater wax moth, *Galleria mellonella* (L.), of 18 different age classes were exposed to various combinations of chilling and space deprivation (Robertson and Dell 1981). The Weibull function was used to calculate the proportion of animals undergoing larval-pupal ecdysis. Analysis of variance was used to test the significance of differences among the time trend statistics for treatments and age classes. Significant differences among time trend statistics were related to interaction between chilling and space deprivation, as well as to the main effect of age class. The pattern observed in most age classes (Fig. 2) was that chilling without space deprivation produced a small delay relative to the unchilled, not space-deprived condition. With space deprivation, however, chilling accelerated pupation compared with space deprivation alone. Contrary to an additive effect, delayed development from space deprivation appeared to be mitigated by chilling.

Time Trends in Mortality After Exposure to Insecticides

In another series of experiments, the residual effectiveness of 11 insecticide formulations to the scolytid pine cone beetle, *Conophthorus ponderosae* Hopkins (= *C. monticolae* Hopkins) was tested (Haverty and Wood 1981). The females of this species attack the host cones and rapidly sever essential connection tissue. A chemical control strategy with the highest probability of success would employ a contact insecticide that acts rapidly and has substantial, effective residual life. Chlorpyrifos and permethrin were judged to be among the best insecticides because of their low LC_{90} values (0.16 and 0.23 g of AI/liter of water, respectively) at 24 h. An LC_{50} value at 24 h does not adequately indicate how fast an efficacious treatment will act. The speed with which various concentrations of a chemical provide the desired level or mortality is of more interest.

Observations at 2-h intervals over 24 h for each dose of the 11 insecticides were recorded, and the time trends for each insecticide were described with the Weibull function (Haverty and Wood 1981). An option of the GERM computer program was used to estimate the time required to reach a particular percentile of change, or mortality level. The times (h)

[1] Copies of GERM, a computer program to summarize data of seed germination tests with an option for fitting the Weibull function, are available from T. R. Dell, Southern Forest Experiment Station, 701 Loyola Avenue, New Orleans, LA 70113. The program description and printout are suited to general applications, but are labelled in terminology specific to seed germination.

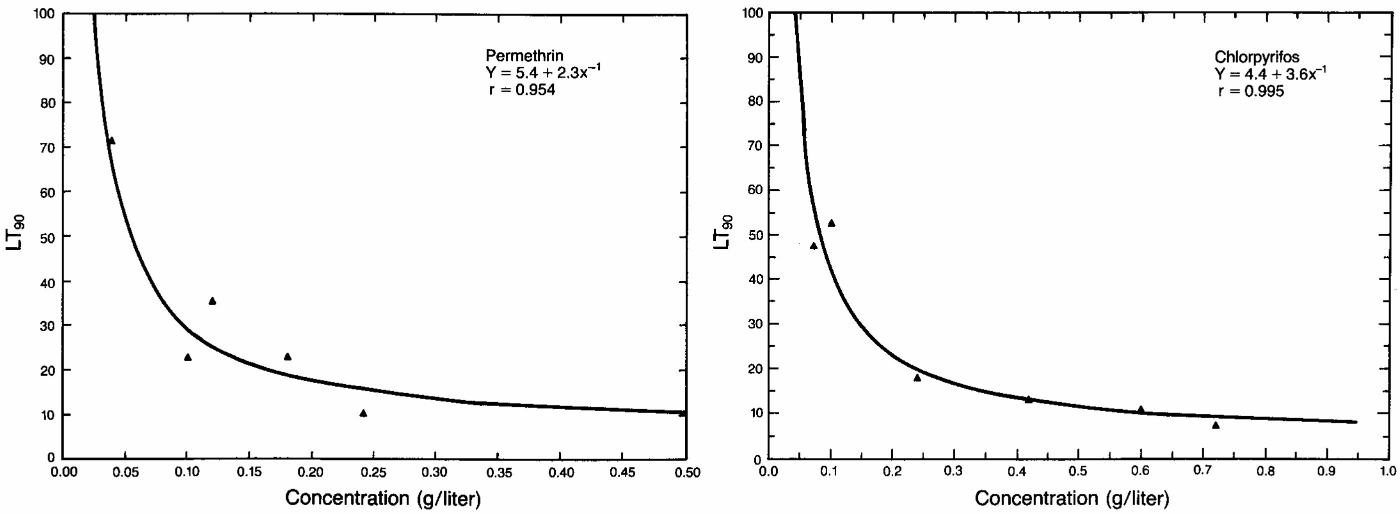

FIG. 3. Response of *C. ponderosae* to chlorpyrifos and permethrin. Hours required to reach 90% mortality were determined with the Weibull function and regressed as a function of concentration.

required to reach 90% mortality for several concentrations of chlorpyrifos and permethrin were estimated with regression techniques (Fig. 3).

The estimates obtained by using the Weibull function to project the amount of time required to achieve a desired level of mortality (i.e., 90%) are directly comparable to estimates of concentration required to obtain a given level of mortality at a fixed time obtained from log-probit analysis. The estimated dose ($\hat{x}$) for Y = 24 h is ca. 0.183 g/liter for chlorpyrifos and 0.124 g/liter for permethrin; each estimate is within the 90% CI for LC_{90} (Haverty and Wood 1981).

Conclusion

Use of the Weibull function adds another dimension to experiments involving the change of test subjects from one state to another. When time trends are calculated, statistical tests among parameters and associated statistics can be performed to determine whether differences are significant. Biological explanations can then be developed to explain the differences.

The types of entomological studies to which this technique has so far proved amenable concern metamorphosis from one life stage to the next and chemical treatment resulting in change of test subjects from one state (i.e., alive) to another (i.e., dead). In experiments with chemical insecticides, time may be of interest in itself, as in the example presented here, or it may be an underlying variable in performing the experiment. For instance, a number of chemicals may be tested to determine their relative toxicities (e.g., Robertson and Haverty 1981). Chemicals of different types have been empirically observed to act at different rates, yet mortality is routinely tallied at a set time. Calculation of time trends for each chemical permits a scientifically based choice of time when treatment effects should be evaluated.

Since the Weibull function is a unimodal distribution, there are instances in which this simple parametric approach is inadequate. Pierce et al. (1979) describe such cases concerned specifically with time to death in which some individuals die as a result of a treatment but 100% mortality attributable to the treatment is never reached; they describe an alternative method by which to analyze such data. Toxicant effects may be even more complicated; our experience with western spruce budworm, *Choristoneura occidentalis* Freeman, demonstrated that some individuals died immediately from handling, some died as a result of treatment, and others survived treatment but died later as a result of unsuccessful metamorphosis (Robertson, unpublished data). Investigators should be aware of these types of confounding components in their evaluation of treatment influences.

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