A RATE SUMMATION MODEL OF TEMPERATURE DEPENDENT DEVELOPMENT WITH STOCHASTIC EXTENSIONS

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Abstract. The studies of population dynamics often involve modeling growth as a function of temperature. The rate summation methodology has perhaps proven to be the most viable approach to such modeling. The majority of the work in rate summation treat the rates as deterministic quantities. There have been some efforts, however, to consider the rates as random variables. The most remarkable work with this posture introduces the concept of "physiological time" as the basis for growth modeling, and provides a comprehensive framework built around that concept. This paper is similar in spirit, but it concentrates on development in "chronological time". The resulting model is, therefore, simple and straightforward.

INTRODUCTION

Models of temperature dependent development are frequently used in population dynamics studies. There are basically three distinct areas of concern in integrating such models in the population dynamics framework.

1. To establish the proper functional relationship between mean development rate and ambient temperature.
2. To develop a distribution model of development times under variable temperature regimes.
3. To incorporate temperature induced and other mortalities to augment the model.

Extensive research has been done in all the three areas and at least a few composite models already exist [e.g., Curry et al. (1978)] that have reported good results.

It is, however, the idea of this paper to highlight the second area alone and present an alternative modeling scheme for temperature dependent development. The scheme builds upon the rate summation approach and includes stochastic variations.

BACKGROUND

The rate summation (rate integration) approach has frequently been demonstrated to be superior in modeling temperature-dependent development. Among others Watson et al. (1973), Ballard (1974) and Stinner et al. (1974) have used this approach with deterministic development rates. Their methods can be best summarized as finding the development time T^ψ under temperature regime ψ such that the equality

$$\sum_{\tau=0}^{T^\psi} \gamma(\psi(\tau))\Delta\tau \simeq 1$$

is satisfied. The term $\gamma(\psi(\tau))$ denotes the mean development rate under temperature $\psi(\tau)$ operational at chronological time τ and $\Delta\tau$ denotes a small increment along the time scale.

Stinner et al. (1975) also drew upon the rate summation approach when they introduced stochastic variation in their development model. Their method used rate summation to estimate four critical points on the distribution of development time which they subsequently obtained by fitting a parametric curve through those points.

A somewhat different treatment of stochastic variation in development modeling can be found in Sharpe et al. (1977). Their method was based on the "physiological time" concept. Physiological time χ at chronological time t was defined as

$$\chi(t) = \sum_{\tau=0}^{t} \gamma(\psi(\tau))\Delta\tau.$$

It was assumed that there existed a unique distribution function $F(\cdot)$ associated with this time scale which in turn described T^ψ, the development time under temperature regime ψ, by the relation $P\{T^\psi \leq t\} = F(\chi(t))$.

The work of Curry et al. (1978a and 1978b) formalized this method and expanded its scope. At present this method seems to be the most attractive in terms of its generality and theoretical soundness.

The method described here shares the same spirit as that of Sharpe et al. (1977) but departs from it considerably in that it attacks the problem of stochastic variations more directly. In its essence it attempts to develop a development distribution on chronological time rather than physiological time. It also does not require the "same shape" property critical to the physiological time model. It must, however, be recognized that this property is intrinsic to many of the modeled systems and can be a convenient apparatus in fully describing a rate process by its mean alone.

MODEL DEVELOPMENT

It is assumed that development under temperature regime ψ may be described by a sequence of rate processes operational during the various phases of the regime. This assumption generally characterizes the rate summation approach. Assuming further that a rate process $\gamma(\psi(t))$ peculiar to temperature $\psi(t)$ at chronological time t is adequately represented by a $N(\mu_{\psi(t)}, \sigma_{\psi(t)}{}^2)$ distribution, the development time T^ψ may be written as

$$T^\psi = \min\{\ t:\ \sum_{\tau=0}^{t} \gamma(\psi(\tau))\ \Delta\tau \geq 1\}\ .$$

If one chooses $\Delta\tau$ to be equal to the elemental time in terms of which the rates are defined, the above equation reduces to

$$T^{\psi} = \min\{ t: \sum_{\tau=0}^{t} \gamma(\psi(\tau)) \geq 1\} .$$

From the above formulation it becomes intuitively clear that the distribution function H (·) of the random variable T^{ψ} at t is given by

$$H(t) = P\{T^{\psi} \leq t\} = P\{ \sum_{\tau=0}^{t} \gamma(\psi(\tau)) \geq 1\} = 1- G_t(1)$$

where $G_t(1)$ is the distribution function of the random variable

$$\sum_{\tau=0}^{t} \gamma(\psi(\tau))$$

at 1. To determine H(t) one only needs to find $G_t(1)$.

Since

$$\chi(t) = \sum_{\tau=0}^{t} \gamma(\psi(\tau)),$$

it is now attempted to identify the distribution function of the random variable $\chi(t)$. This can be done relatively easily once the underlying relationship among the rate processes $\gamma(\psi(t))$ at t=0,1,2... becomes clear. To seek this clarification one once again resorts to a second assumption inherent to the rate summation approach which advocates development as being linear over time. This assumption of linearity points now to a perfect linear association between the consecutive random rate processes. In other words, the random variables $\gamma(\psi(t))$ and $\gamma(\psi(t+1))$ for all t's may be considered to have a perfect positive correlation.

Any $\gamma(\psi(t))$ under these circumstances can be written as $\gamma(\psi(t)) = \mu_{\psi(t)} + k\sigma_{\psi(t)}$ where k is a N(0,1) random variable which applies uniformly to all t's. Thus

$$\chi(t) = \sum_{\tau=0}^{t} \gamma(\psi(\tau)) = \sum_{\tau=0}^{t} \mu_{\psi(\tau)} + k \sum_{\tau=0}^{t} \sigma_{\psi(\tau)}$$

is a random variable which follows the

$$N\left(\sum_{\tau=0}^{t} \mu_{\psi(\tau)}, \sum_{\tau=0}^{t} \sigma_{\psi(\tau)}{}^{2}\right)$$

distribution. Therefore

$$G_t(1) = \Phi\left(\frac{1 - \sum_{\tau=0}^{t} \mu_{\psi(\tau)}}{\sum_{\tau=0}^{t} \sigma_{\psi(\tau)}}\right)$$

where $\Phi(\cdot)$ is the left tail area under a N(0,1) probability density function. To summarize, it can then be written that

$$H(t) = 1-\Phi\left(\frac{1 - \sum_{\tau=0}^{t} \mu_{\psi(\tau)}}{\sum_{\tau=0}^{t} \sigma_{\psi(\tau)}}\right)$$

The above model at this point can easily be implemented along with an iterative methodology to get a complete description of H(·). The error function erf(·) may be used to aid in the evaluation of $\Phi(\cdot)$.

DISCUSSIONS

A limitation to the model proposed here is perhaps that of the normality assumption. Though the normal distribution conforms to the symmetry exhibited by most rate processes, other symmetric distributions (e.g., quadratic in Sharpe et al. (1977)) have sometimes resulted in better models. A second weakness of the normal distribution is its unboundedness which stands in stark contrast to the boundedness of all development rate distribution.

It is felt, however, that both these shortcomings have very limited implications with regard to the efficacy of the model. In most cases normal distributions provide adequate fit to the rate processes and for all practical purposes its unboundedness should not interfere with its usage. On the contrary, the normal distribution is well-studied and does immensely simplify the analytical aspects of the model.

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