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# Application of Time Scales Calculus to the Growth and Development in Populations of *Stomoxys calcitrans* (Diptera: Muscidae)

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**Abstract**

Typical methods of sampling for groups of insects utilize purely temporal sampling intervals. However, arthropod developmental parameters are known to be directly proportional to measures of accumulated temperature. It has recently been demonstrated that population growth models for arthropods exhibit a higher degree of correlation with empirical data when values derived from temporal sampling regimes are transformed into a function of accumulated degree days above a lower developmental threshold. Here we considered the possibility of further enhancing the accuracy of population parameter estimates by employing alternative sampling methods which incorporate temperature accumulation. We isolate the object of analysis by designing discrete models with time scales calculus. By testing two models in which the sampling interval is the experimental variable, we demonstrate that a regime which consists of sampling events evenly spaced with respect

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to degree days yields growth rate estimates with smaller total residual error. With these results, we propose that acquisition of insect population data could more effectively be conducted by employing a system in which sampling frequency varies with temperature regimes.

**AMS Subject Classifications:** 39, 92.
**Keywords:** Time scales calculus, discrete modeling, degree days, population modeling, sampling regimes, stable fly.

# 1 Introduction

Management decisions about agricultural pests rely on population parameters. These parameters must be estimated using field-collected data. Typical strategies for field sampling involve collecting data in regular time intervals (i.e., weekly, monthly). In the methods of virtually all projects noted by authors of this study, sampling of pest insects in agricultural settings occurred at regular temporal intervals (weekly, bi-weekly, monthly) [12]. Even studies that sought to estimate temporal variability in arthropod abundance or efficiency of capture (e.g., [15, 19]) employed regular spacing of samples in time.

Poikilotherm populations, most notably insects, are characterized by their physiological responses to fluctuations in temperature. The nature of the temperature - dependent development of these organisms has been studied and modeled extensively [4, 6, 9, 13, 14, 16]. Methods for estimating degree days were first introduced by Arnold [2] and later modified by others [1, 4, 17], and they follow the assumption that insects do not develop below a given minimum temperature threshold. Degree days are calculated by estimating the accumulated temperature above that threshold for a given time and can be used to predict development for plants, insects, and other organisms with limited ability to regulate temperature. The importance of degree days to insect development is incorporated into fields such as forensic entomology [10], and although it is a well-understood concept in relation to agricultural pests [12], sampling for pest insects remains mostly temporally-based. However, the degree day transformation of Beresford and Sutcliffe [6] yielded improved statistical correlation and enhanced parameter estimates in a population model of *Stomoxys calcitrans* L. (stable fly) in dairy operations in Canada. Motivated by the possibility of enhancing models of poikilotherm population growth, Beresford and Sutcliffe [6] considered a temperature-dependent modification of temporally-sampled field data. Their results provided support for the incorporation of seasonal temperature accumulation for poikilotherm field data analysis, proposing that temporally-sampled field data be based on a degree day-based time series [5, 6]. This degree day transformation yielded improved statistical correlation and enhanced parameter estimates in a population model of *S. calcitrans* [6].

Despite these encouraging results, current models do not include temperature considerations in field procedures and field data analysis, opting instead to sample at regular time intervals. Difference equations presents itself as a potential means by which to conduct such analysis. However, the irregularity of the sampling events which is inherent in conventional regimes cannot be represented and varied via difference equations.

Instead, we employ time scales calculus in order to most effectively assess candidate regimes. The theory of time scales calculus was developed with the objective of unifying and extending continuous and discrete analysis [11]. In certain applications, time scales provides a means by which a set of data points at arbitrary intervals can be efficiently analyzed. Therefore, these methods have been used in a diverse group of applications including economic, automotive, and biological studies [3, 18]. One of the main tools of times scales calculus is the graininess function. This function will play a key role in our models by representing the spacing between sampling events. Unlike difference equation models, this graininess need not be constant.

Using data generated from the work of Beresford and Sutcliffe [5], we wanted to further analyze population parameters using time scales calculus. Specifically, we estimate the error sums of squares (ESS) in two different models of sampling regimes. The first model represents a population estimate based on data that are collected regularly with respect to time (variable graininess model). The second model represents a population estimate based on data that are collected regularly with respect to temperature (constant graininess model). Our objective was to use ESS of two models as an indicator of which would produce more accurate population estimates, and we hypothesized that the constant graininess model would yield lower ESS values.

# 2 Methods

First we make precise what is meant by a degree day.

**Definition 2.1** (See [8])**.** A degree day is a unit of measurement equal to a difference of one degree between the mean outdoor temperature on a certain day and a reference temperature.

In our case, the reference temperatures were taken to be the lower threshold of development, $10^\circ$C, and the upper threshold of development, $30^\circ$C. A sine curve was used to approximate the temperatures for each day, with the area under the curve integrated to approximate accumulated degree day [1, 17]. To evaluate the effects of incorporating measures of temperature accumulation into sampling regime design, we constructed two discrete models representing a conventional, temporal sampling regime (variable graininess model) and an idealized degree day regime (constant graininess model) of exponential growth. The models were so named to emphasize that when biologists sample regularly with respect to weeks, they are sampling irregularly with respect to temperature accumulation. This is illustrated in Figure 2.1. While conventional discrete analysis is conducted via difference equations, flexibility with regards to sampling frequency demanded a more versatile methodology. Using time scales calculus, we are

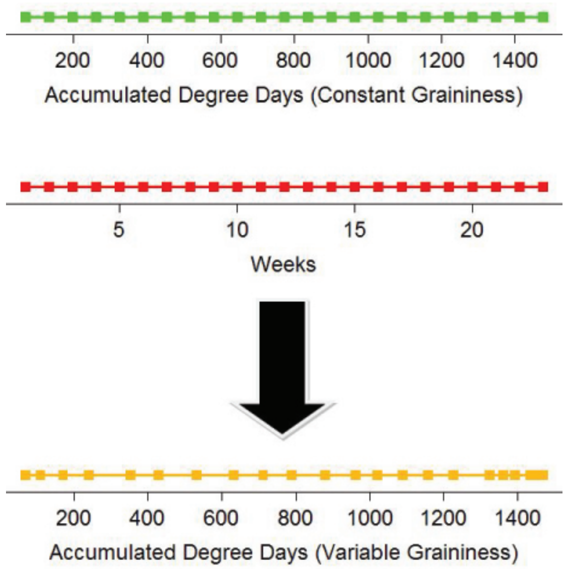


Figure 2.1: Transformation from weeks to degree days (DD); when biologists sample regularly with respect to weeks, they are sampling irregularly with respect to temperature; we test a theoretical sampling regime in which data are collected regularly with respect to accumulated temperature.

able to test the functional output effects of altering sampling patterns and thereby assess the efficacy of a variety of regimes.

There are a number of characteristics that are desirable in such a model. As seen in Figure 2.1, it is necessary to develop models in which interval length can be varied and tested as an experimental variable. Thus, our circumstances demand that the number of individuals in a population, $N$, be modeled as a function of interval length $\mu(t)$, while a growth rate parameter, $p$, is necessary to provide a characteristic trend. Additionally, in the anticipation of error analysis we note that only isolated points in the time series (namely those points characterizing a single sampling event) will be considered. Given these stipulations, our analysis is well suited for discrete methods.

This introduction contains the fundamental ideas concerning differentiation and exponential functions on time scales. The material presented in this section is proved in detail in Bohner and Peterson [7].

**Definition 2.2.** A time scale, denoted, $\mathbb{T}$, is an arbitrary nonempty closed subset of the real numbers.

We now introduce the forward jump operator, $\sigma$, and the graininess function, $\mu$. These functions characterize points in the time scale and are critical in our model formulation.

**Definition 2.3.** Let $\mathbb{T}$ be a time scale and let $t \in \mathbb{T}$. We define the forward jump operator

$\sigma : \mathbb{T} \to \mathbb{T}$ by

$$\sigma(t) := \inf\{s \in \mathbb{T} : s > t\},$$

and the backward jump operator $\rho : \mathbb{T} \to \mathbb{T}$ by

$$\rho(t) := \sup\{s \in \mathbb{T} : s < t\}.$$

In this definition we put $\inf \emptyset = \sup \mathbb{T}$ and $\sup \emptyset = \inf \mathbb{T}$, where $\emptyset$ denotes the empty set. A point $t$ is right-scattered if $\sigma(t) > t$ and left-scattered if $\rho(t) < t$. Points that are right-scattered and left-scattered at the same time are isolated. Also, if $t < \sup \mathbb{T}$ and $\sigma(t) = t$, then $t$ is called right dense, and if $t > \inf \mathbb{T}$ and $\rho(t) = t$, then $t$ is left-dense. Points that are left and right dense at the same time are dense. Finally, the graininess function $\mu : \mathbb{T} \to [0, \infty)$ is defined by $\mu(t) = \sigma(t) - t$.

Throughout this paper, we consider the isolated time scale $\mathbb{T} = \{t_0, t_1, \cdots, t_m\}$, which contains a finite number of points where $t_n$ represents a specified sampling event. We let $\mathbb{T}^\kappa = \mathbb{T} \backslash \{t_m\}$.

**Theorem 2.4.** *Let $\mathbb{T} = \{t_0, t_1, \cdots, t_m\}$, $f : \mathbb{T} \to \mathbb{R}$ be a function, and let $t \in \mathbb{T}^\kappa$. Then we define the delta derivative $f^\Delta(t)$ as*

$$f^\Delta(t) = \frac{f(\sigma(t)) - f(t)}{\mu(t)}.$$

Before we define a generalized exponential function, we introduce a preliminary definition.

**Definition 2.5.** A function $p : \mathbb{T} \to \mathbb{R}$ is regressive provided $1 + \mu(t)p(t) \neq 0$ for all $t \in \mathbb{T}^\kappa$. The set of regressive functions is denoted $\mathcal{R}$.

**Theorem 2.6.** *Assume $p \in \mathcal{R}$. Then the exponential function $e_p(t, t_0)$ is the unique solution to the initial value problem $y^\Delta = p(t)y, y(t_0) = 1$.*

For our model development, we assume that population growth of insects is exponential [6, 9, 14]. Thus, by Theorem 2.6, we consider

$$N^\Delta = pN, N(t_0) = N_0$$

where $N_0$ is the initial number of individuals in the population, $N(t)$ is the projected number of individuals in a population after a specified period of time, $t$, and $p$ is the growth rate conveyed as number of flies per degree day. Applying Theorem 2.4, we arrive at the variable graininess model

$$N(t_n) = N_0 \prod_{i=0}^{n-1} (1 + \mu(t_i)p), \quad 1 \leq n \leq m. \tag{2.1}$$

For the constant graininess model in which sampling interval length is consistent during a growing season, we consider an analysis of data sets which contain only isolated points at regular intervals. Therefore, the time scale we are working with has a constant graininess. To arrive at a model of growth for this sampling system, we consider the special case when $\mu(t_i) = h$, for all $i \in \{0, 1, 2, \cdots, m-1\}$. When this condition is applied to (2.1), we arrive at the constant graininess model, an exponential model which accommodates evenly-spaced data sets:

$$N(t) = N_0(1 + hp)^{\frac{t}{h}}. \tag{2.2}$$

The time scales for equations (2.1) and (2.2) are represented in Figure 2.1 as the bottom and top domains, respectively. To illustrate the effects of altering sampling methods, we compare a variable graininess model to a constant graininess model. Time scales modeling of *Stomoxys calcitrans* population dynamics, based on field data was tested on the models represented by (2.1) and (2.2). The data are weekly collections of stable flies caught on sticky traps [5] set at six dairy farms in south-central Ontario from May 18 to November 25 in 1998, and May 3 to December 3 in 1999. Two traps were placed at each farm near cattle pens. Traps were collected each week so that the number of stable flies caught at each farm could be counted. To determine growth rates, $p$, we used a least squares optimization method.

To assess the variable graininess and constant graininess models represented by (2.1) and (2.2), respectively, in representing actual field data, we consider the residual, or error, sum of squares (ESS). To test for statistically significant improvement, we compared field means of ESS from the variable graininess model to ESS from the constant graininess model in both 1998 and 1999 with paired $t$-Tests.

The constant graininess model, (2.2), is representative of a theoretical regime in which sampling is implemented over constant intervals with respect to temperature accumulation. For this model, the number of degree days applied for the constant sampling interval length was determined by maintaining the same number of sampling events as the original data to allow for comparison of total residual error values. We interpolated the provided field data because the original data was obtained by sampling irregularly with respect to temperature. To do this interpolation, we used the secant lines between the actual data and the corresponding points of accumulated degree days.

# 3 Results

The variable graininess model resulted in an average ESS of 16.82 $\pm$ 4.37 (mean $\pm$ S.E.) in 1998 and 16.42 $\pm$ 3.72 in 1999 (Table 3.1). The constant graininess model resulted in a decrease in ESS for every field and a significant average decrease by 65% in 1998 (*df*= 5, *t*= 2.57, *p*= 0.006) and 58% in 1999 (*df*= 4, *t*= 2.78, *p*= 0.020) (Table 3.1).

| 1998 | | | |
|---|---|---|---|
| Site | Variable ESS | Constant ESS | Total % Change |
| 1 | 30.41 | 20.75 | 31.77% |
| 2 | 27.28 | 7.35 | 73.06% |
| 3 | 5.51 | 1.34 | 75.68% |
| 4 | 13.11 | 3.55 | 72.92% |
| 5 | 11.95 | 2.21 | 81.51% |
| 6 | 12.64 | 5.66 | 52.22% |
| Ave(s.e.): | 16.82(4.37) | 6.81(3.21) | 65.03% |
| 1999 | | | |
| Site | Variable ESS | Constant ESS | Total % Change |
| 1 | 17.43 | 12.41 | 28.80 % |
| 2 | 23.66 | 7.68 | 67.54% |
| 3 | 20.05 | 12.28 | 38.75% |
| 4 | 16.96 | 3.96 | 76.65% |
| 5 | 4.01 | 0.81 | 79.80% |
| Ave(s.e.): | 16.42(3.72) | 7.43(2.55) | 58.31% |

Table 3.1: Comparison of error sum of squares for sampling data using variable and constant graininess. The average change shown in the last column indicates an improvement when sampling is conducted seasonally instead of temporally. ESS= error sum of squares.

Figure 3.1 shows a representative subset of sites and a graphical representation of improvement in ESS from the variable graininess model compared to the constant graininess model.

# 4 Discussion

Statistical analysis of the variable and constant graininess models allowed us to evaluate sampling regimes on the basis of their capacity to produce representative population parameters. Results from error analysis revealed that the variable graininess model yielded greater total residual error than the constant graininess model (see Table 3.1). Specific residuals observed for the constant graininess model were smaller than temporally proximate residuals for the variable graininess model. From this, we suggest that sampling regimes which incorporate measures of accumulated temperature into the time series governing the frequency of sampling events will produce parameter estimates with enhanced accuracy. We have provided additional support for the claim that graphical representations of temporally sampled data for poikilotherms are inherently flawed, particularly in multivoltine species. In fact, it is reasonable to conclude that the magnitude of error observed in analysis of temporally sampled data is directly depen-

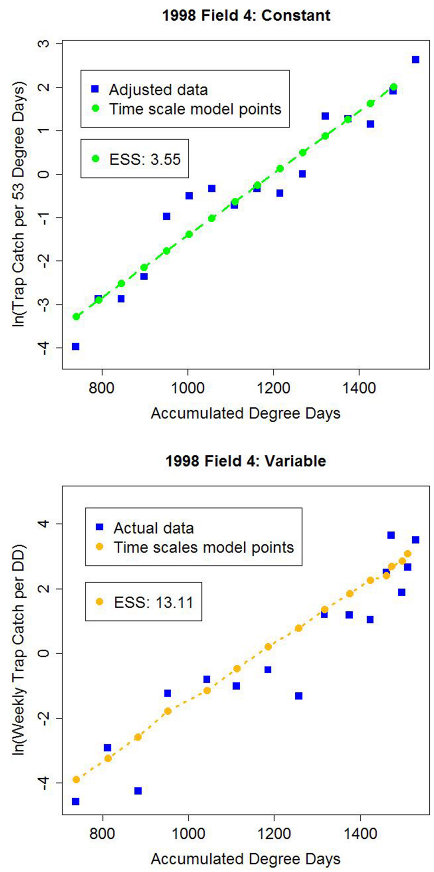


Figure 3.1: Model fit to field data showing the comparison of variable (below) and constant (above) graininess from sampling. Data were adjusted using interpolations for constant graininess analysis. Data were taken from Beresford and Sutcliffe [5], 1998 data from their Field 4. ESS= error sum of squares.

dent on the variation in temperature that a particular population experiences in a given sampling season. Therefore, sampling in poikilothermic populations experiencing tropical climates will not demand significant modifications, but regimes for populations in temperate regions will likely be improved by temperature-related restructuring.

These results indicate that there is a need for further research. With evidence that adjusting collection methods to arrive at regular sampling frequencies with respect to a population's activity will improve population level models, the field is ripe for a host of new regime modifications informed by mathematical inquiry.

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