

# Relationship Between Temperature and Developmental Rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and Its Prey *Tetranychus mcdanieli* (Acarina: Tetranychidae)

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**ABSTRACT** Temperature affects insect and mite development, allowing species-specific traits including optimal temperature and low and high temperature thresholds to be observed. Development rate models and biological parameters estimated from them can help determining if synchrony exists between pests and natural enemies. We studied development of the coccinellid *Stethorus punctillum* Weise and the spider mite *Tetranychus mcdanieli* McGregor at 12 constant temperatures ranging 10–38°C ( $\pm 0.5^\circ\text{C}$ ), and modeled their development rates as a function of temperature. This predator-prey complex is typical of red raspberry, *Rubus idaeus* L., in Quebec, which is characterized by a short season. Eleven published models were compared for accuracy in predicting development rate of all stages of both species, and estimating their temperature thresholds and optima. The spider mite developed to the adult stage in the 14–36°C range, compared with 14–34°C for the coccinellid. Males and females did not differ, and the development rates steadily increased from 14 to 30°C, leveling off in the range 34–36°C for the spider mite, or 30–32°C for its predator. Most models were rejected for failure to satisfy criteria of goodness-of-fit and estimable temperature threshold parameters. The Lactin-2 model for *T. mcdanieli* and the Brière-1 model for *S. punctillum*, were superior at estimating low temperature threshold, which is critical where temperatures are frequently low in the spring, and were separately fitted to all development stages of both organisms. Based on the predictable early spring development of *S. punctillum* and *T. mcdanieli*, the results indicate potential synchrony between them.

**KEY WORDS** *Tetranychus mcdanieli*, *Stethorus punctillum*, developmental rate, temperature, non-linear models, predator-prey synchrony

KNOWLEDGE OF INSECT and mite adaptations to climatic conditions plays an essential role in pest management, specifically in helping to predict the timing of development, reproduction, and dormancy or migration (Nechols et al. 1999). In biological control, details concerning such responses are useful to select natural enemies that are best adapted to conditions favoring target pests (Rosen and Huffaker 1983, Obrycki and Kring 1998). Biological control, whether using the introduction, conservation or augmentation approaches, is facilitated when the climatic responses of biocontrol agents are known, especially temperature.

Temperature is a critical abiotic factor influencing the dynamics of mite and insect pests and their natural enemies (Huffaker et al. 1999 and references herein). Temperature sets the limits of biological activity in

arthropods, such that low and high temperature thresholds, and optimal temperature can be estimated for all major life processes. Natural enemies and their host/prey may have different thermal limits and effective temperature range for survival, development, reproduction, and mobility. Thermal characteristics may vary between species (Frazer and McGregor 1992, Honek 1996), populations (Campbell et al. 1974, Lee and Elliott 1998), developmental stages (Honek and Kocourek 1988), and with other ecological factors such as food source (Gilbert and Raworth 1996).

Temperature also acts as a driver of arthropod life processes, where within a specific range, a temperature change results in a proportional increase or decrease of the rate of any given process (Cossins and Bowler 1987). This effect of temperature can be described by specific rate functions of temperature for survival, reproduction, population growth, and development, which are used in predicting natural enemy interactions with pests (Jervis and Copland 1996). Developmental rate, expressed as the reciprocal of time taken to change from one stage to another (Cossins and Bowler 1987), is nil at the low temperature threshold, increases with temperature and levels

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off at the optimum, and then decreases rapidly as the high threshold is approached. This relationship is curvilinear near extremes, but approximately linear at moderate temperatures (Wagner et al. 1984). A variety of rate functions or models have been proposed to describe the relationship between temperature and arthropod development (Logan et al. 1976, Sharpe and DeMichele 1977, Wagner et al. 1984, Lamb 1992, Lactin et al. 1995, Brière et al. 1999). They vary with respect to parameter number and basic assumptions about temperature effects near lower and upper limits (see appendix). Temperature-driven rate models are most often used to predict the activity and seasonal population dynamics of pests and natural enemies in field situations (Frazer and McGregor 1992, Lamb 1992, Brière and Pracros 1998) but they also help determining suitable conditions for mass rearing of natural enemies (Rodríguez-Saona and Miller 1999).

Distributed throughout North America, the McDaniel spider mite, *Tetranychus mcdanieli* McGregor is the most important tetranychid pest of red raspberry in Quebec (Roy et al. 1999), where it damages fruiting canes in late spring to midsummer, and primocanes in late summer to early fall. Prolonged susceptibility to damage implies season-long spider mite control, which is not provided by current acaricides (Roy et al. 1999). Alternative controls are needed to develop an integrated control program emphasizing biological control. In other horticultural crops including almonds, apples, citrus and strawberries, spider mite biocontrol is achieved by managing phytoseiid mite or *Stethorus* coccinellid predators (Tanigoshi et al. 1983, Hoy 1985, McMurtry 1985, van de Vrie 1985, Kogan et al. 1999).

In a recent study aiming to identify natural enemies of the McDaniel spider mite, the coccinellid *S. punctillum* Weise, a palearctic species inadvertently established in eastern Canada (Putnam 1955), was an important predator in raspberries (Roy et al. 1999). As specialist predators, *Stethorus* spp. can effectively control spider mite populations, as shown for *S. punctillum* on cotton and vineyards in Europe (Kapur 1948) and citrus in Japan (Yang et al. 1996); *S. punctum punctum* LeConte on apple in USA (Hull 1977); and *S. punctum picipes* Casey on avocado in the USA (McMurtry and Johnson 1966, Tanigoshi 1973). The key biological attributes of *S. punctillum* as a spider mite predator have rarely been studied, and its potential against *T. mcdanieli* is unknown.

The objective of this study was to develop knowledge of the thermal characteristics of populations of *S. punctillum* and its prey *T. mcdanieli* collected in Quebec, as a prerequisite to developing a biological control program in raspberry. The development rate of all stages of both species was measured at 12 constant temperatures ranging 10–38°C, thus spanning the expected field conditions during a typical raspberry-growing season in southern Quebec. With the data at hand, we tested 11 temperature-driven rate models chosen among the most commonly used, and compared them not only with respect to accuracy at predicting the development rate, but also at estimating

related biological parameters of *S. punctillum* and *T. mcdanieli*. Although temperature is only one of the ecological factors in predator-prey dynamics, its strong effects on development is particularly important in affecting generation time and thus evaluating the ability of a predator to track a prey population over several generations by its numerical response.

## Materials and Methods

**Rearing Methods and Experimental Conditions.** Experiments were conducted in 1994 and 1995 in Conviron PGR15 (Controlled Environment, Winnipeg) growth chambers. *Tetranychus mcdanieli* and *S. punctillum* were originally collected in 1993 from a raspberry field near Quebec City, Canada (46° 59' N, 71° 29' W). The ensuing colonies of *T. mcdanieli* and *S. punctillum* were maintained on red raspberry, *Rubus idaeus* L. 'Killarney', and European cucumber, 'Thompson' at 24°C and a photoperiod of 16:8 (L:D) h. Voucher specimens are preserved in the insect collection of the Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec, Sainte-Foy, Québec. Temperature and relative humidity in each growth chamber were recorded continuously with an integrated data logger.

Experimental arenas consisted of 2.0-cm-diameter raspberry leaf disks placed upside down on submerged cotton wool in individual 5.0-cm-diameter petri dishes. The dishes were covered with lids ventilated with a 1.0 mm mesh. Spider mites and coccinellids were individually handled with a small brush. Observations were made with a stereomicroscope under a cold light source.

**Development and Survivorship of Immatures.** To obtain synchronized eggs, spider mite or coccinellid females were incubated at 25°C on raspberry leaf discs for 5 h. Newly laid eggs of *S. punctillum* and *T. mcdanieli* were then placed individually on leaf disks. Upon hatching, *S. punctillum* larvae were fed with excess ( $\approx 300$ ) *T. mcdanieli* of various stages. Insects and mites were placed in growth chambers programmed to control temperature at 10, 12, 14, 16, 20, 24, 28, 30, 32, 34, 36, or  $38 \pm 0.5^\circ\text{C}$ , which covered the full range of constant temperatures allowing complete development of both species. The ambient relative humidity alternated between 45 and 65% during the light and dark cycles, respectively. Fluorescent lamps yielding  $175 \mu\text{E s}^{-1} \text{m}^{-2}$  within each chamber provided a 16-h daily photophase. Sixty individuals were tested per temperature regime.

Progress in development and survival was assessed every 3 to 12 h, depending on the temperature. For calculation purposes, events were assumed to have occurred at the midpoint between two consecutive observations. Fresh leaf disks were provided every 2 or 3 d, until maturity was reached. The survival rate and duration were obtained for all immature stages. After hatching, *T. mcdanieli* develops through larva, protonymph and deutonymph stages, with a terminal period of quiescence called protochrysalis, deutochrysalis, and teleiochrysalis, respectively; and *S. punctillum*

**Table 1.** Capacity of 11 developmental rate models to estimate three important biological parameters, and specific method of estimation when applicable

| Model                | Low temp threshold | Optimal temp       | High temp threshold |
|----------------------|--------------------|--------------------|---------------------|
| Linear               | $x$ at $y = 0$     | —                  | —                   |
| Logan-6              | —                  | $T_L - \Delta T$   | $T_L$               |
| Logan-10             | —                  | $T_L - \Delta T$   | $T_L$               |
| Sharpe and DeMichele | —                  | $x$ at $dy/dx = 0$ | —                   |
| Taylor               | —                  | $T_m$              | —                   |
| Lamb                 | — <sup>a</sup>     | $T_m$              | —                   |
| Hilbert and Logan    | $T_0$              | $T_L - \Delta T$   | $T_L$               |
| Lactin-1             | —                  | $T_L - \Delta T$   | $T_L$               |
| Lactin-2             | $x$ at $y = 0$     | $T_L - \Delta T$   | $T_L$               |
| Brière-1             | $T_0$              | $x$ at $dy/dx = 0$ | $T_L$               |
| Brière-2             | $T_0$              | $x$ at $dy/dx = 0$ | $T_L$               |

<sup>a</sup> Lamb (1992) proposed a replacement for low temperature threshold defined as the temperature at which the developmental rate is 8% of the maximum developmental rate, but this parameter does not estimate developmental threshold in absolute terms.

developed through four larval stages, and the pupal stage. The sex of each adult was determined.

**Developmental Rate Models.** *Description of Models.* We compared the performance of one linear and 10 nonlinear developmental rate models, chosen because they are the most commonly used for that purpose. The nonlinear models were two by Logan et al. (1976), one by Taylor (1981), one by Sharpe and DeMichele (1977), one by Hilbert and Logan (1983), one by Lamb (Lamb et al. 1984, Lamb 1992), two by Lactin et al. (1995) and two by Brière et al. (1999). These models are described in more details in the *Appendix*.

*Criteria of Model Selection.* The following criteria were used to assess the performance of each model:

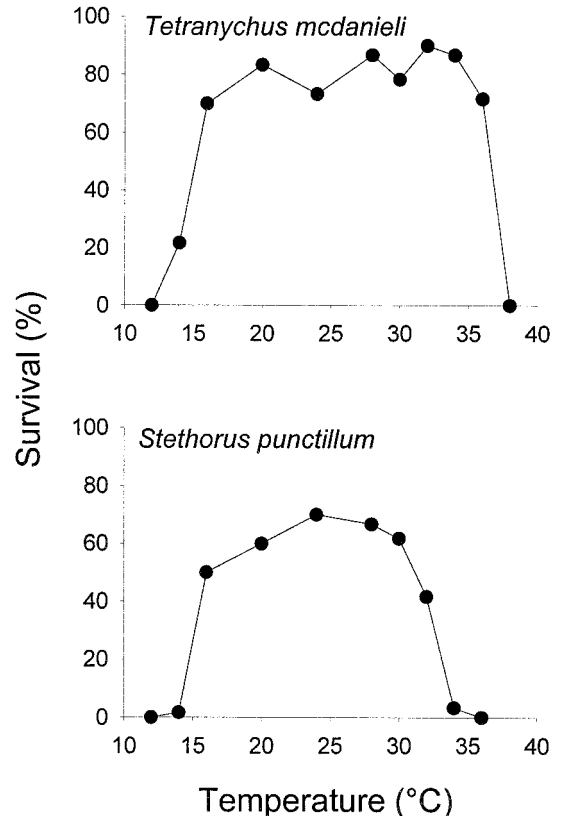
(1) The model should describe the data accurately. Two statistics were used to evaluate accuracy: the adjusted coefficient of determination ( $R^2$ ), and the residual sum of squares (RSS), which provide complementary information on goodness-of-fit and usefulness for predicting observations (Draper and Smith 1998).

(2) The model should allow estimation of parameters with biological significance (Brière et al. 1999). For development, the key biological parameters needed are the low temperature threshold, optimal temperature and high temperature threshold, as defined previously. In the context of our study of organisms developing in cool temperate regions, a useful model preferably should provide a low temperature threshold estimate.

**Statistical Methods.** For each species, differences among sexes for developmental times at various constant temperatures were tested for significance by analysis of variance (ANOVA) using the general linear model procedure of SAS (SAS Institute 1989). For each stage developmental time variation with temperature was confirmed by regression using the exponential model  $y = a + be^{(-T/c)}$  (SAS Institute 1989). Then, the means of reciprocals of developmental time for each stage, and at each temperature, were used to fit the developmental rate models. The curves were fitted by iterative nonlinear regression based on the Marquardt algorithm (SAS Institute 1989) on mean developmental rates weighted by sample size ( $n$ -weighed). Except for the Sharpe and DeMichele

model (1977), all nonlinear models have parameters that can be interpreted graphically, which is useful to allow initial parameter estimation (Brière et al. 1999). For the degree-day linear model, the developmental rate was regressed against temperature using a least squares linear regression (Draper and Smith 1998).

Depending on the model, the biological parameters were either directly estimated, derived from other parameters within the model, or they were obtained from the value of  $x$  at  $y = 0$  or the value of  $x$  at  $dy/dx =$



**Fig. 1.** Effect of temperature on survival from egg to adult (%) of *Tetranychus mcdanieli* and *Stethorus punctillum*.

**Table 2.** Developmental time (d  $\pm$  SE) of immature stages of *T. mcdanieli* at 11 constant temperatures

| Temp, °C | Egg            | Larva         | Protonymph    | Deutonymph    | Total Immature |
|----------|----------------|---------------|---------------|---------------|----------------|
| 12       | 25.3 $\pm$ 0.3 | —             | —             | —             | —              |
| 14       | 17.1 $\pm$ 0.9 | 8.2 $\pm$ 1.7 | 6.7 $\pm$ 1.5 | 7.0 $\pm$ 0.6 | 39.0 $\pm$ 3.9 |
| 16       | 12.0 $\pm$ 0.4 | 6.0 $\pm$ 0.7 | 4.8 $\pm$ 0.6 | 6.0 $\pm$ 0.7 | 28.8 $\pm$ 1.2 |
| 20       | 6.9 $\pm$ 0.4  | 3.1 $\pm$ 0.5 | 2.8 $\pm$ 0.4 | 3.4 $\pm$ 0.5 | 16.3 $\pm$ 1.0 |
| 24       | 4.0 $\pm$ 0.2  | 2.4 $\pm$ 0.4 | 2.0 $\pm$ 0.4 | 2.3 $\pm$ 0.3 | 11.1 $\pm$ 0.8 |
| 28       | 3.1 $\pm$ 0.1  | 1.5 $\pm$ 0.3 | 1.3 $\pm$ 0.3 | 1.7 $\pm$ 0.4 | 7.6 $\pm$ 0.9  |
| 30       | 2.7 $\pm$ 0.1  | 1.2 $\pm$ 0.2 | 0.9 $\pm$ 0.1 | 1.4 $\pm$ 0.2 | 6.3 $\pm$ 0.4  |
| 32       | 2.5 $\pm$ 0.1  | 1.2 $\pm$ 0.3 | 1.2 $\pm$ 0.3 | 1.6 $\pm$ 0.4 | 6.5 $\pm$ 0.8  |
| 34       | 2.3 $\pm$ 0.1  | 1.1 $\pm$ 0.2 | 0.9 $\pm$ 0.1 | 1.2 $\pm$ 0.2 | 5.5 $\pm$ 0.3  |
| 36       | 2.3 $\pm$ 0.1  | 1.2 $\pm$ 0.2 | 0.9 $\pm$ 0.2 | 1.1 $\pm$ 0.2 | 5.5 $\pm$ 0.3  |
| 38       | 2.6 $\pm$ 0.2  | 1.7 $\pm$ 0.0 | —             | —             | —              |

$n = 60$  at experiment initiation; a dash indicates mortality or arrested development; the exponential regression  $y = a + be^{(-T/c)}$  was fitted to each stage ( $r^2 = 0.99$  and  $P < 0.0001$  in all cases).

0 (Table 1). In the latter two cases the variance of these parameters was obtained by the Delta method (Agresti 1990). The maximum likelihood ratio test (Lehmann 1994) was applied to determine whether or not the biological parameters differed among growth stages, and if observed values (midpoint between the two closest experimental temperatures) significantly departed from model estimates.

### Results

**Survival of Immatures.** *T. mcdanieli* successfully developed to adult between 14 and 36°C, but failed at 10, 12, and 38°C. (Fig. 1). The optimal temperature for immature survival ranged between 16 and 36°C. The highest mortality occurred during the egg stage at extreme temperatures (data not shown). Survival for all other stages between 14 and 36°C ranged from 71.4 to 100%.

*Stethorus punctillum* successfully developed to the adult stage between 14°C and 34°C, but survival was low at both ends of the temperature range (Fig. 1). The optimal range for immature survival was between 16 and 32°C. Eggs failed to hatch at 12 and 36°C. Similar to *T. mcdanieli*, *S. punctillum* mortality occurred mainly during the egg stage (data not shown).

**Development Time.** ANOVA on development time of both species at all temperatures revealed no difference between males and females (data not shown;  $P > 0.05$ ), hence averages were computed using pooled data. Table 2 presents the average development times of all stages of *T. mcdanieli* at 11 constant temperatures. The length of each stage decreased and levelled

off, following the exponential model. In the range 14–36°C, the length of the egg stage averaged 42% of total.

The development time of all stages of *S. punctillum* at eight constant temperatures is presented in Table 3. General trends noted above for *T. mcdanieli* also apply to *S. punctillum*. In the range 14–34°C, the length of the egg stage was 28%, and the pupal stage was 23% of total development.

**Model Accuracy and Precision.** For *T. mcdanieli*, the adjusted  $R^2$  varied between 0.76 and 0.98 (Table 4, because the  $R^2$  and RSS trends were similar to those observed for total immature development, only the latter are presented). The linear, Taylor, Brière-1, Lactin-1 and Logan-6 models do not accurately predict the developmental rate of *T. mcdanieli* at temperatures  $< 20$  and  $> 30$ °C. Adding one parameter to the Logan-6, Lactin-1 and Brière-1 models, provides for more accurate prediction. For example, the  $R^2$  value of the four-parameter Brière-2 model (0.98) is substantially higher than the three-parameter Brière-1 model (0.83).

The Brière-2, Hilbert and Logan, Lactin-2, Logan-10, and Lamb models all have adjusted  $R^2$  higher than 0.96 (Table 4), and also had the smallest RSS. Therefore, with *T. mcdanieli*, the linear, Taylor, Sharpe and DeMichele, Logan-6, Lactin-1, and Brière-1 models are rejected because they failed to meet the criterion for high model accuracy.

For *S. punctillum*, the adjusted  $R^2$  ranged 0.84–0.99 (Table 4). With  $R^2$  values below 0.97, the linear, Taylor and Sharpe and DeMichele models were rejected. Contrary to *T. mcdanieli*, the addition of one param-

**Table 3.** Developmental time (d  $\pm$  SE) of immature stages of *S. punctillum* fed on *T. mcdanieli* at eight constant temperatures

| Temp, °C | Egg            | 1st Instar    | 2nd Instar    | 3rd Instar    | 4th Instar     | Pupa           | Total immature |
|----------|----------------|---------------|---------------|---------------|----------------|----------------|----------------|
| 14       | 21.1 $\pm$ 0.0 | 8.4 $\pm$ 0.0 | 7.0 $\pm$ 0.0 | 6.0 $\pm$ 0.0 | 11.1 $\pm$ 0.0 | 15.0 $\pm$ 0.0 | 68.5 $\pm$ 0.0 |
| 16       | 14.4 $\pm$ 0.9 | 6.4 $\pm$ 1.0 | 4.2 $\pm$ 0.9 | 4.9 $\pm$ 0.7 | 8.4 $\pm$ 0.9  | 10.7 $\pm$ 0.8 | 48.9 $\pm$ 3.0 |
| 20       | 7.8 $\pm$ 0.5  | 3.4 $\pm$ 0.4 | 2.1 $\pm$ 0.4 | 2.4 $\pm$ 0.5 | 4.3 $\pm$ 0.5  | 6.1 $\pm$ 0.3  | 26.1 $\pm$ 0.9 |
| 24       | 4.8 $\pm$ 0.3  | 2.0 $\pm$ 0.2 | 1.6 $\pm$ 0.2 | 1.7 $\pm$ 0.3 | 3.0 $\pm$ 0.3  | 4.1 $\pm$ 0.3  | 17.1 $\pm$ 0.6 |
| 28       | 3.6 $\pm$ 0.2  | 1.5 $\pm$ 0.4 | 1.1 $\pm$ 0.3 | 1.3 $\pm$ 0.2 | 2.3 $\pm$ 0.3  | 2.9 $\pm$ 0.1  | 12.7 $\pm$ 0.6 |
| 30       | 3.4 $\pm$ 0.2  | 1.2 $\pm$ 0.2 | 1.0 $\pm$ 0.1 | 1.2 $\pm$ 0.2 | 2.0 $\pm$ 0.2  | 2.8 $\pm$ 0.2  | 11.5 $\pm$ 0.2 |
| 32       | 3.2 $\pm$ 0.2  | 1.4 $\pm$ 0.2 | 1.0 $\pm$ 0.2 | 1.3 $\pm$ 0.3 | 2.2 $\pm$ 0.4  | 2.7 $\pm$ 0.2  | 11.8 $\pm$ 0.6 |
| 34       | 3.1 $\pm$ 0.2  | 1.6 $\pm$ 0.2 | 1.0 $\pm$ 0.0 | 1.4 $\pm$ 0.0 | 2.1 $\pm$ 0.7  | 3.0 $\pm$ 0.0  | 12.1 $\pm$ 0.7 |

$n = 60$  at experiment initiation; the exponential regression  $y = a + be^{(-T/c)}$  was fitted to each stage ( $r^2 = 0.99$  and  $P < 0.0001$  in all cases).

**Table 4.** Comparison of 11 developmental rate models based on the number of parameters (NPAR), the adjusted coefficient of determination ( $R^2$ ), and the residual sum of squares (RSS) for predicting total immature development of *T. mcdanieli* and *S. punctillum*

| Model                | NPAR           | <i>Tetranychus mcdanieli</i> |         | <i>Stethorus punctillum</i> |         |
|----------------------|----------------|------------------------------|---------|-----------------------------|---------|
|                      |                | $R^2$                        | RSS     | $R^2$                       | RSS     |
| Linear               | 2              | 0.76643                      | 0.00619 | 0.84468                     | 0.00067 |
| Logan-6              | 4              | 0.88410                      | 0.00230 | 0.97173                     | 0.00009 |
| Logan-10             | 5              | 0.97744                      | 0.00037 | 0.99215                     | 0.00002 |
| Sharpe and DeMichele | 4 <sup>a</sup> | 0.93536                      | 0.00124 | 0.93503                     | 0.00020 |
| Taylor               | 3              | 0.81881                      | 0.00420 | 0.93337                     | 0.00025 |
| Lamb                 | 4              | 0.98044                      | 0.00039 | 0.98971                     | 0.00003 |
| Hilbert and Logan    | 5              | 0.96906                      | 0.00051 | 0.98928                     | 0.00003 |
| Lactin-1             | 3              | 0.89344                      | 0.00247 | 0.97625                     | 0.00090 |
| Lactin-2             | 4              | 0.96580                      | 0.00068 | 0.98936                     | 0.00003 |
| Brière-1             | 3              | 0.83545                      | 0.00382 | 0.97649                     | 0.00009 |
| Brière-2             | 4              | 0.98001                      | 0.00040 | 0.98328                     | 0.00005 |

<sup>a</sup> Wagner et al. (1984) identified the four parameter-reduced model, as the most appropriate.

eter to the Logan-6, Lactin-1 and Brière-1 models only slightly improved their fitting for *S. punctillum* development. For example, with the four-parameter Brière-2 model  $R^2$  (0.983) is <1% better than the three-parameter Brière-1 version (0.976), whereas  $R^2$  increased by 15% with *T. mcdanieli*. For *S. punctillum*, the models retained using the RSS criterion also were the same as using the  $R^2$ .

**Biological Parameters.** The Logan-6, Logan-10, Sharpe and DeMichele, Taylor, and Lactin-1 models do not estimate a low temperature threshold; and although the Lamb model proposed a replacement for the low temperature threshold, it did not estimate it as defined earlier. Also, the linear model does not provide either the optimal temperature or the high temperature threshold (Table 1). Therefore, all these models fail to satisfy our second criterion. In contrast, the Hilbert and Logan, Lactin-2, Brière-1, and Brière-2 models, all provide estimates for low and high temperature thresholds, and optimal temperature.

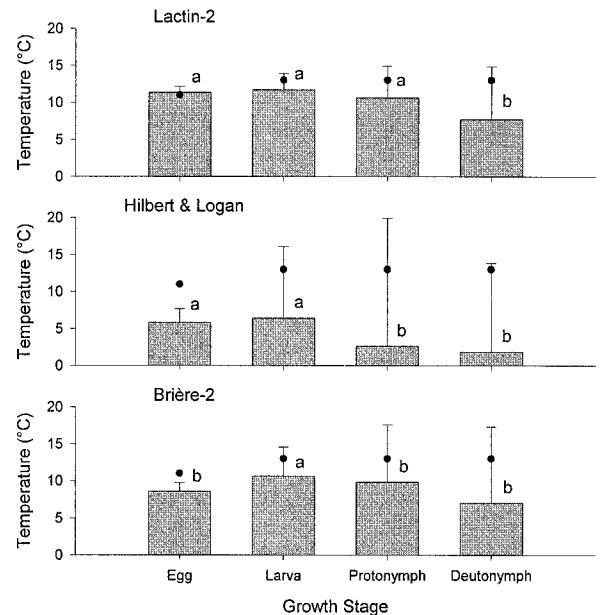
Predicted low temperature threshold estimates of the three models meeting both selection criteria were compared with predicted values in Fig. 2 for *T. mcdanieli*. The observed values are within the 95% confidence interval of the model estimate for all stages, except the egg for the Hilbert and Logan and Brière-2 models. Still, the low thresholds seem to be best predicted by the Lactin-2 model. They differed significantly among stages (maximum likelihood ratio test,  $P < 0.01$ ), but these differences did not translate into any clear trend or pattern.

The estimates of the optimal temperature and high temperature threshold of *T. mcdanieli* are similar to observed values for the three models (data not shown). The observed optimal temperatures for fast development of *T. mcdanieli* ranged within 34–36°C and did not differ among growth stages ( $P > 0.05$ ). The observed high temperature thresholds ranged 38–40°C. For all three models the predicted value of the high temperature threshold of the egg stage was significantly higher than values predicted for the other stages ( $P < 0.01$ ).

For *S. punctillum*, both criteria were met by four models, i.e., the Hilbert and Logan, Lactin-2, Brière-1, and Brière-2. The observed values of the low temper-

ature threshold are best predicted with the Brière-1 model (Fig. 3). Again, this parameter differed significantly ( $P < 0.01$ ) among stages, but with no consistent trend.

With these four models, differences between predicted and observed values of optimal temperature and high temperature threshold for *S. punctillum* are not as large as for the low temperature threshold (data not shown). The observed optimal temperature for fast development of *S. punctillum* ranged 34–36°C, with significant variation among stages ( $P < 0.01$ ) but without any specific trend. The observed high temperature threshold of 36.0°C did not vary among stages ( $P > 0.05$ ).



**Fig. 2.** Observed (●) and predicted values (bars = estimate + 95% confidence interval) of low temperature threshold of *Tetranychus mcdanieli* based on three developmental rate models. Within models, estimates with the same letter do not differ significantly according to the maximum likelihood ratio test ( $\alpha = 0.05$ ).

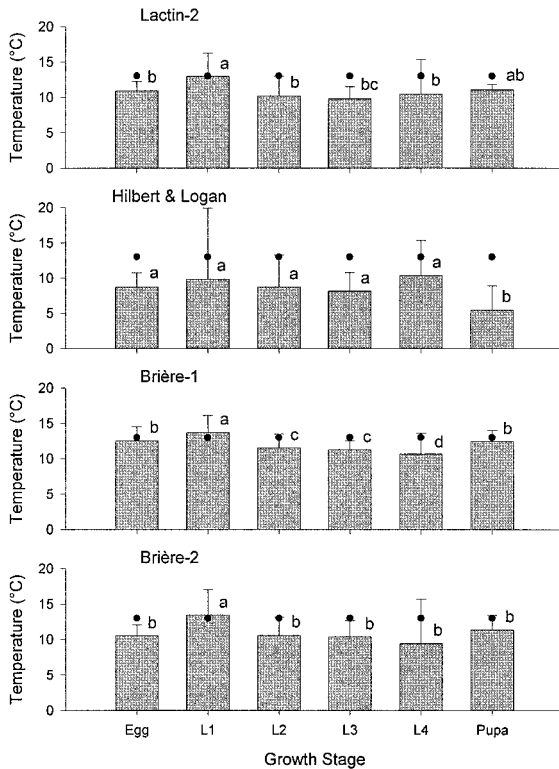


Fig. 3. Observed (●) and predicted values (bars = estimate + 95% confidence interval) of low temperature threshold of *Stethorus punctillum* based on four developmental rate models. Within models, estimates with the same letter do not differ significantly according to the maximum likelihood ratio test ( $\alpha = 0.05$ ).

Given similar estimation of the optimal temperature and high temperature thresholds by three models for *T. mcdanieli* and four for *S. punctillum*, accuracy at predicting the low temperature threshold was referred to for final selection. This threshold was more closely predicted by the Lactin-2 model for *T. mcdanieli* and the Brière-1 model for *S. punctillum*, hence they were chosen and their fit to data are presented in Figs. 4 and 5, respectively. They were separately fitted to all stages as the maximum likelihood ratio test indicated that the value of the parameters do, in some instances (see above), vary among stages.

### Discussion

No other study has covered the full range of temperatures that are suitable to the development and survival of *T. mcdanieli* and *S. punctillum* in North America. Tanigoshi et al. (1975) studied the effects of temperature on development, reproduction, and population growth of *T. mcdanieli* from Washington State on lima beans. Concerning *Stethorus* coccinellids, temperature effects on development are available for *S. madecassus* Chazeau (Chazeau 1974), *S. loxtoni* Britton and Lee (Richardson 1977), and *S. punctum picipes* (Tanigoshi 1973). In North America, Putnam (1955)

reported development data for *S. punctillum* at a single temperature. *T. mcdanieli* survival and development data reported here partially agree with Tanigoshi et al. (1975) results on Pacific Northwest populations on apple. They reported development at 10 and 38°C, whereas we did not obtain any development under 14°C and over 36°C, suggesting differing temperature adaptations between the two populations. The effect of temperature on *S. punctillum* development has been studied in Europe by Bravenboer (1959) at 21–23°C; and Berker (1958) in the 15–35°C interval, which does not extend sufficiently low to fully cover the climatic conditions prevailing in Quebec.

Numerous studies show that the egg stage of *Tetranychus* spp. lasts longer, by a factor of approximately two, than any active stage (Crooker 1985), similar to our results (Table 2). This implies a long window of opportunity for *S. punctillum* adults, which preferentially feed on spider mite eggs. As was expected, *S. punctillum* had a much longer development than its *T. mcdanieli* prey: for example 26.1 d at 20°C is 10 d longer than *T. mcdanieli* (Tables 2 and 3). This major difference plus the temperature range for high survival to maturity being markedly wider for the prey (16–36°C) than the predator (20–32°C) (Fig. 1), suggest that, in the long-term over a number of generations, the prey should have numerical advantage over the predator.

The curvilinear developmental rate-temperature relation for both species is typical of many other insects and mites (Brière and Pracros 1998). It can be adequately described by several nonlinear rate models for each species, but only one was retained in each case based on goodness-of-fit, and estimable temperature-related biological parameters. For *T. mcdanieli*, six of the 11 models tested did not fit the data well. Surprisingly, the Logan-6 model, which was fitted by Logan et al. (1976) to data from a Washington State population of *T. mcdanieli*, did not provide a good fit. Among the five other models, the Lamb and the Logan-10 models provided good fit, but predicted development rate approaches zero asymptotically and no low temperature threshold can be estimated (Brière and Pracros 1998). In contrast, the Brière-2, Hilbert and Logan and Lactin-2 models enabled the development rate curve to intersect the temperature axis. The low temperature threshold estimates for specific stages were most accurate using the Lactin-2 model (Fig. 2). All in all, we conclude that the Lactin-2 model best describes the relationship of development rate to temperature for this *T. mcdanieli* population. Lactin et al. (1995) stated that this model is preferable when temperatures are frequently near the low threshold, which is the case early in the season in Quebec. This model also was found highly efficient in modeling the rice root aphid, *Rhopalosiphum rufiabdominalis* (Sasaki) (Tsai and Liu 1998).

For *S. punctillum*, eight models fitted the data well, and adequately predicted developmental rates. The Lamb, Logan-6, Logan-10, and Lactin-1 models were rejected for failure to estimate a low temperature threshold as generally defined. The low temperature thresholds estimates of the Lactin-2, Brière-1 and Bri-

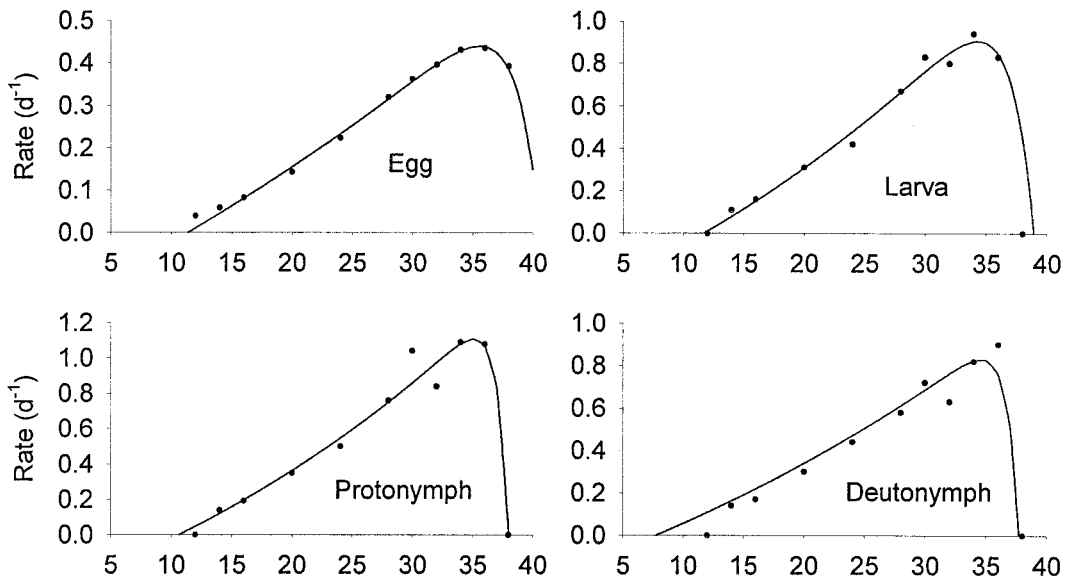


Fig. 4. Fitting the Lactin-2 model to developmental rate data for the egg, larva, protonymph and deutonymph stages of *Tetranychus mcdanieli* as a function of temperature ( $^{\circ}\text{C}$ ). Dots represent observed rates.

ère-2 models were close (Fig. 3), however, the Brière-1 model requires three parameters versus four for the other two models. A model should meet the general criterion of parsimony (see e.g., Lamb et al. 1984), and contain as few parameters as possible given that goodness-of-fit and other (e.g., biological) criteria are met.

Although the Lactin-2 model for *T. mcdanieli* and the Brière-1 model for *S. punctillum* seem to be the best and satisfactorily estimated the optimal temperatures and the high temperature thresholds, they sometimes provided inaccurate estimation of the low temperature threshold. Development may be observed at the estimated low temperature threshold (e.g., *T. mcdanieli* eggs, Fig. 4; and *S. punctillum* first instar, Fig. 5). In other instances, no development was observed over several degrees above the estimated low temperature threshold (e.g., *T. mcdanieli* deutonymph, Fig. 4; and *S. punctillum* fourth instar, Fig. 5).

Problems in estimating low temperature thresholds may be due to intrinsic model weaknesses in fitting data across such broad temperature ranges. The processes that cause heat stress and death at high temperature may be basically different from those that affect development and chilling injury at low temperature. Inaccuracies might also be due to experimental error, or greater variability of individuals within a population, when exposed to extreme conditions. Additional sampling at the left-hand side of the curve, by including more experimental temperatures and more individuals might provide more precise estimation of the low temperature threshold.

In addition, the dual objective of selecting a useful model for predicting development rate and estimating life history parameters may not be met efficiently by

a single model. However, in practice using a single model is preferable, which may justify compromising to some degree. Our criteria resulted in choosing different best models for *T. mcdanieli* and *S. punctillum* but these criteria could include the requirement for a unique model for both species.

Our results indicate potential synchrony between the two organisms based on their predictable early spring development, so long as overwintered adults emerge from postdiapause and start reproducing simultaneously. The low threshold estimate of *T. mcdanieli* eggs is  $11.35^{\circ}\text{C}$  (Figs. 2 and 4). At a daily average of  $12^{\circ}\text{C}$ , the first eggs laid would hatch in 25 d (Table 2), but unless average temperature increases by a few degrees, the spider mite would not develop further. At  $14^{\circ}\text{C}$ , *T. mcdanieli* eggs would hatch in 17 d, and the larvae would then become protonymphs (Crooker 1985). The low threshold estimate of *S. punctillum* is  $12.0^{\circ}\text{C}$  (Figs. 3 and 5) and the first eggs could reach the first instar in 22 d at  $14^{\circ}\text{C}$  if prey are available. Thus, at  $14^{\circ}\text{C}$ , by the time *T. mcdanieli* would reach the protonymph stage, the first instar of *S. punctillum* would have developed and be able to feed on mite eggs and protonymphs, the preferred prey stages of the closely related *S. punctum* (Houck 1980). Our data suggest that these relationships would hold at higher average temperatures as well (Tables 2 and 3). Thus, a raspberry system with *S. punctillum* should be less exposed to unrepressed early feeding by spider mite protonymphs and deutonymphs, as predatory stages of the coccinellid should be active simultaneously.

This work described the development-temperature relationships of Quebec populations *T. mcdanieli* and *S. punctillum* under the broad range of temperatures generally prevailing in this region, and estimated their key bioclimatic parameters. Nevertheless, more

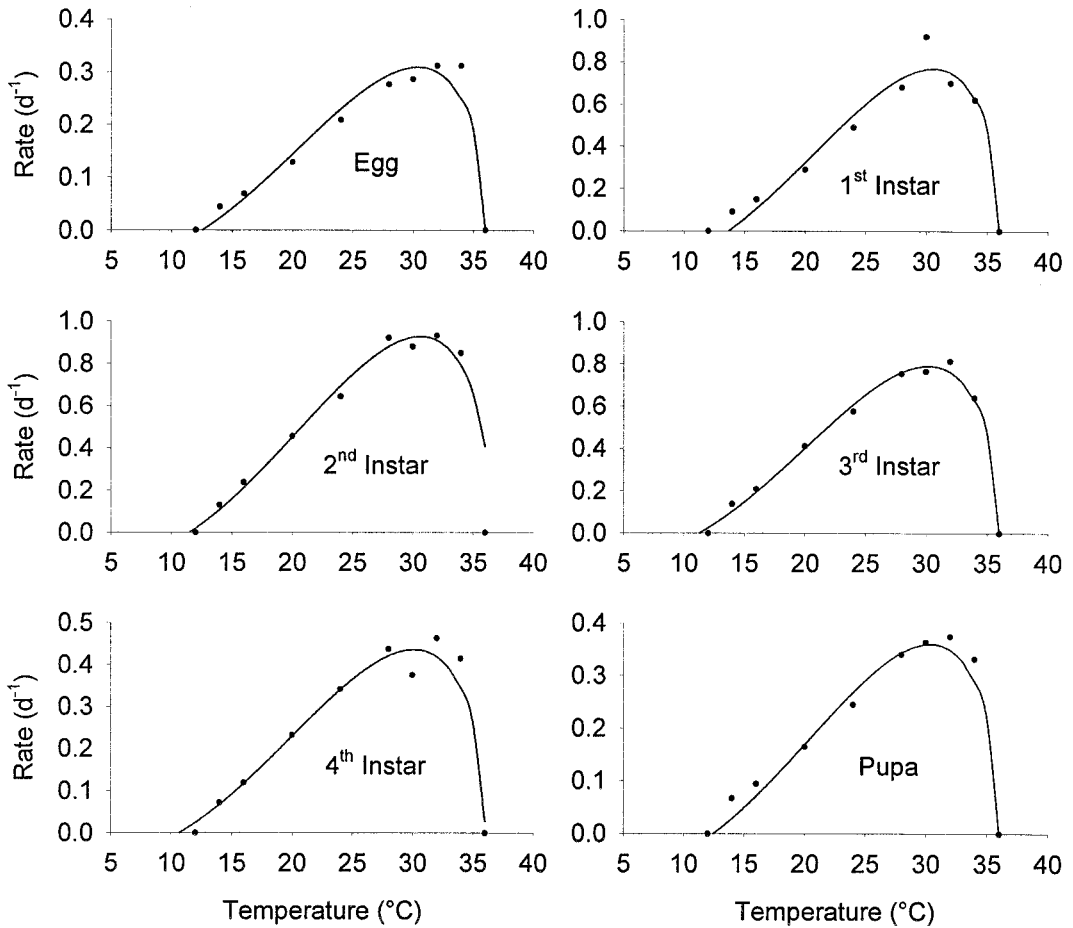


Fig. 5. Fitting the Brière-1 model to developmental rate data for the egg, first, second, third, fourth larval and pupal stages of *Stethorus punctillum* as a function of temperature ( $^{\circ}\text{C}$ ). Dots represent observed rates.

knowledge of their adaptations at temperatures close to the low threshold would be important. Poikilotherms often are well adapted to survive and even develop to some extent during long periods of cold temperatures (Brière et al. 1999, Liu and Meng 1999). Also, although it appears that early synchrony between the two organisms would allow the coccinellid to impact the spider mite protonymphs and deutonymphs, the assumption that *S. punctillum* would prey on these *T. mcdanieli* stages like *S. punctum* on *T. urticae* Koch remains to be verified. Knowledge of the predatory behavior of *S. punctillum* is very limited (e.g., Rott and Ponsonby 2000).

Finally, *T. mcdanieli* and *S. punctillum* are multivoltine, implying that the effect of temperature on reproductive potential and especially their intrinsic rate of natural increase ( $r_m$ ) would be most useful for predicting their long-term interactions over several generations. A better set of key ecological parameters would then be available to determine the potential usefulness and role of *S. punctillum* in an integrated

red raspberry production system under cool climatic conditions.

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### Appendix: Models

The linear model or degree-day model is commonly used to determine thermal constants (degree-days) and lower development thresholds from developmental rate of arthropod stages (Campbell et al. 1974, Frazer and McGregor 1992, Rencken and Pringle 1998, Lopez-Arroyo et al. 1999). The linear model is defined as follows:

$$D(T) = a + bT,$$

where  $T$  is the rearing temperature ( $^{\circ}\text{C}$ ),  $a$  is the developmental rate at  $T = 0^{\circ}\text{C}$ , and  $b$  is the slope of the regression line.

The two models developed by Logan et al. (1976) are defined by combining two functions with matched asymptotes, and are usually referred to as Logan models six and 10. These empirical models have been widely used in biological control studies (Cloutier et al. 1995, van Rijn et al. 1995). The Logan-6 model is defined by the equation

$$D(T) = \psi (e^{(\rho T)} - e^{(\rho T_L - (T_L - T)/\Delta T)})$$

where  $T$  is the rearing temperature ( $^{\circ}\text{C}$ ),  $\Psi$  is the maximum developmental rate,  $\rho$  is a constant defining the rate at optimal temperature,  $T_L$  is the lethal maximum temperature, and  $\Delta T$  is the temperature range over which physiological breakdown becomes the overriding influence. The Logan-10 model is defined as follow,

$$D(T) = \alpha ((1/(1 + ke(-\rho T))) - e^{-(T_L - T)/\Delta T}),$$

where  $\alpha$ , and  $k$  are empirical constants, and  $T$ ,  $\rho$ ,  $T_L$ , and  $\Delta T$  are as in the Logan-6 model.

The Sharpe and DeMichele (1977) biophysical model, reparametrized by Schoolfield et al. (1981) is based on enzyme reaction rate theory, and all six parameters are assumed to have a thermodynamic biochemical interpretation (Wagner et al. 1984). This model has been used to predict development of arthropod preys and predators (Orr and Obyrcki 1990, Stäubli Dreyer et al. 1997). The Sharpe and DeMichele model is defined by the equation,

$$D(T) = (\rho T/298.15 e^{(\Delta H_1/1.987 (1/298.15 - 1/T))}) / (1 + (e^{(\Delta H_2/1.987 (1/T_{1/2} - 1/T))}) + (e^{(\Delta H_3/1.987 (1/T_{1/3} - 1/T))})),$$

where  $T$  is the rearing temperature ( $^{\circ}\text{K}$ ),  $\rho$  is the developmental rate at  $25^{\circ}\text{C}$ ,  $\Delta H_A$  is the enthalpy of activation of reaction,  $\Delta H_L$  is the change in enthalpy at low temperature,  $T_{1/2L}$  is the temperature at which the enzyme for the low temperature portion is 1/2 active,  $\Delta H_H$  is the change in enthalpy at high temperature,  $T_{1/2H}$  is the temperature at which the enzyme for the high temperature portion is 1/2 active.

The Taylor model (1981) is a simple normal function written as follows:

$$D(T) = R_m e^{(-.5((T - T_m)/T_{\sigma})^2)},$$

where  $T$  is the rearing temperature ( $^{\circ}\text{C}$ ),  $R_m$  is the maximum development rate at temperature  $T$ ,  $T_m$  is the temperature where the development rate is highest, and  $T_{\sigma}$  is a shape parameter giving the spread of the curve.

The Lamb model (Lamb et al.1984, Lamb 1992) is an asymmetrical normal function modified from Taylor (1981) and is defined as follows:

$$D(T) = R_m e^{(-.5((T - T_m)/T_{\sigma L})^2)} \text{ for } T \leq T_m$$

and

$$D(T) = R_m e^{(-.5((T - T_m)/T_{\sigma H})^2)} \text{ for } T > T_m,$$

where  $T$ ,  $R_m$ , and  $T_m$  are as in Taylor's equation.  $T_{\sigma L}$  is a shape parameter giving the spread of the curve for  $T \leq T_m$ , and,  $T_{\sigma H}$  is a shape parameter giving the spread of the curve for  $T > T_m$ .

The Hilbert and Logan model (1983), a combination of sigmoid and exponential equations, was formulated to improve the Logan model by providing a lower threshold of development. This model has been used recently by Scott and Yeoh (1999) to predict the development of an aphid with biocontrol potential against a weed. The Hilbert and Logan model is defined as follows:

$$D(T) = \Psi \left( \frac{(T - T_0)^2}{(T - T_0)^2 + d^2} \right) - e^{-(T_L - (T - T_0))/\Delta T)},$$

where  $T$ ,  $\Psi$ ,  $T_L$ , and  $\Delta T$  are as in the Logan-6 model,  $T_0$  and  $d$  are empirical parameters.

In 1995, Lactin et al. proposed two modifications of the Logan-6 model. First, they eliminated a redundant parameter to obtain the Lactin-1 model. Second, they incorporated an intercept parameter, which allows estimation of a low temperature threshold for development, resulting in Lactin-2 model. These models have recently been used by Brière and Pracros (1998) and by Tsai and Liu (1998). The Lactin-1 model is defined as follows:

$$D(T) = e^{(\rho T)} - e^{(\rho T_L - (T_L - T)/\Delta T)},$$

and the Lactin-2 model is,

$$D(T) = e^{(\rho T)} - e^{(\rho T_L - (T_L - T)/\Delta T)} + \lambda.$$

In both Lactin's models,  $T$ ,  $\rho$ ,  $T_L$ , and  $\Delta T$  are as in the Logan-6 model, and in the Lactin-2 model  $\lambda$  forces the curve to intercept the y-axis at a value below zero and thus allows estimation of a low temperature threshold.

More recently, Brière et al. (1999) have proposed two more models with a nonlinear part at low and high temperatures and a linear portion at intermediate temperatures. The Brière-1 model is defined as follows:

$$D(T) = a T (T - T_0) (T_L - T)^{1/2}$$

and the Brière-2 model is as follows:

$$D(T) = a T (T - T_0) (T_L - T)^{(1/d)}.$$

In both models  $T$  is the rearing temperature ( $^{\circ}\text{C}$ ),  $a$  is an empirical constant,  $T_0$  is the low temperature development threshold,  $T_L$  is the lethal temperature threshold, and in the Brière-2 model  $d$  is an empirical constant.