



Effect of temperature on intrinsic rates of natural increase (r_m) of a coccinellid and its spider mite prey

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Abstract. The intrinsic rate of natural increase (r_m) is useful to estimate the population growth potential of insects and mites, which may help predict the outcome of pest-natural enemy interactions. This study was conducted to determine how 12 constant temperature regimes between 10–38 °C (± 0.5 °C) may differentially affect the r_m of the McDaniel spider mite, *Tetranychus mcdanieli* McGregor (Acarina: Tetranychidae), a common pest of raspberry, and its coccinellid predator, *Stethorus punctillum* Weise (Coleoptera: Coccinellidae). *Tetranychus mcdanieli* survived to maturity in the 14–36 °C range, compared to the 14–32 °C range for *S. punctillum*. Survival above 24 °C remained high for the spider mite, but decreased markedly for the coccinellid. *Tetranychus mcdanieli*'s range for reproduction was similar to its survival range, but *S. punctillum* failed to reproduce at 14 °C and reproduced only poorly at 16 °C. Offspring production peaked at 24 °C for both *T. mcdanieli* (average 152 eggs per female), and *S. punctillum* (280 eggs per female). At all temperatures suitable for reproduction, female longevity of the coccinellid was greater than the spider mite, which was characterized by earlier/faster reproduction than the coccinellid. As temperature increased, the r_m followed a typical asymmetrical dome-shape pattern, with maximum values of 0.196 d⁻¹ and 0.385 d⁻¹ at 30 °C and 34 °C, for *S. punctillum* and *T. mcdanieli*, respectively. For each species, the r_m -temperature relation was successfully modelled using a curvilinear regression equation previously shown to predict development rate. In both species, the development rate response to temperature has a major influence on the temperature- r_m relationship. In the 16–32 °C range suitable for population growth of both species, the r_m of *T. mcdanieli* was 1.9 (30 °C) to 8 (16 °C) times greater than *S. punctillum*. These growth potential ratios are consistently in favor of the prey, suggesting a limitation of the coccinellid with respect to its capacity to track *T. mcdanieli* populations. However, under short season conditions, the inferior reproductive dynamics of *S. punctillum*'s vs. spider mite prey should not have a prevailing influence in determining impact, and may be compensated by high voracity in combination with a strong aggregative response.

Key words: Acarina, biological control, Coccinellidae, Coleoptera, intrinsic rate of natural increase, raspberry, *Stethorus punctillum*, *Tetranychus mcdanieli*, temperature, Tetranychidae

Introduction

The intrinsic rate of natural increase (r_m) is a key demographic parameter useful for predicting the population growth potential of an animal under given environmental conditions (Andrewartha and Birch, 1954; Ricklefs and Miller, 2000; Southwood and Henderson, 2000). Transposed to predator-prey population dynamics, the outcome of a given interaction is likely to depend on the relative r_m of the protagonists (Janssen and Sabelis, 1992). In theory, a predator that has a population growth rate equal to or greater than its prey should efficiently regulate the population of its prey (e.g. Sabelis, 1992). In biological control practice, r_m values are increasingly used as a mean of selecting promising biocontrol candidates on the basis of their reproductive potential and to predict the outcome of pest-natural enemy interactions once a biocontrol agent is introduced in a system (Jervis and Copland, 1996; Dent, 1997).

The r_m can be estimated from life table data under standardized laboratory conditions (Southwood and Henderson, 2000). A number of extrinsic and intrinsic factors have been shown to affect r_m and related demographic parameters. For arthropods, temperature is a key determinant of r_m since developmental period, longevity, pre-reproductive delay, fecundity, fertility and other life history parameters are highly correlated with temperature (Birch, 1948). There are numerous examples where the impact of temperature on r_m has been considered for herbivore (Sabelis, 1985a, 1991; van Rijn et al., 1995), predator (Sabelis, 1985b; Cloutier et al., 1995; Stäubli Dreyer et al., 1997; Lopez-Arroyo et al., 1999; Dixon, 2000), and parasitoid species (Biswas and Singh, 1997). Contrary to the developmental rate, for which a variety of more or less complex models have been developed (Wagner, 1984; Lamb, 1992; Lactin et al., 1995; Brière et al., 1999), the relationship between temperature and r_m has not been extensively modelled.

Siddiqui et al. (1973) developed predictive equations of r_m , as a function of temperature by combining the equation of Pradhan (1946) for the rate of development, with an empirically established relationship between $1/r_m$ and development rate, but the relationship did not hold at temperatures above 30 °C. Logan et al. (1976) developed two exponential models to predict arthropod development and population growth rates as a function of temperature. Using constant temperature data, they parameterised temperature-driven models of development and reproduction of *Tetranychus mcdanieli* McGregor (Acarina: Tetranychidae) on bean, which allowed their inclusion in an apple pest management model. They also obtained a good fit of both models for several published development rate-temperature data sets of various pests and natural enemies (Logan et al., 1976). Cloutier et al. (1995) used a Logan model to predict the rate of population increase of

two thrips predators, *Amblyseius cucumeris* (Oudemans) and *Orius insidiosus* (Say). The rate of population increase was accurately predicted under cool and warm fluctuating temperature regimes for *A. cucumeris* and slightly less efficiently for *O. insidiosus*. Despite the reduced accuracy of estimation at the two extremes of the temperature response curve, modelling population growth rates (r_m) can be helpful to compare temperature-dependent population dynamics of predator species and prey. They can further be used to predict temperature regimes for which a predator can develop and reproduce at least as fast as its prey, which should be favorable to biological control.

The objective of this study was to examine how temperature affects r_m of the McDaniel spider mite and its coccinellid predator. *Tetranychus mcdanieli* is a significant pest of raspberries in Quebec, Canada. Like most tetranychid species (Sabelis, 1985a), *T. mcdanieli* is a typical colonizing species characterized by short generation time, a high capacity for population growth, and cyclic dispersal. The coccinellid *Stethorus punctillum* Weise (Coleoptera: Coccinellidae), a palearctic species accidentally introduced in eastern Canada (Putnam, 1955), has become one of the most common predators of spider mites in cultivated raspberry in Quebec (Roy et al., 1999). *Stethorus punctillum* adults and larvae are specialized predators of tetranychid mites. In a previous study, we examined the relationship between temperature and developmental rate in *T. mcdanieli* and *S. punctillum* and found a similar curvilinear temperature-dependent response for development of both species (Roy et al., 2002). However, the mean developmental rate of the prey was 1.5 to 2.4 times faster than that of the predator, over a large range of temperature, suggesting a similar relation between their population growth potentials.

Under laboratory conditions, we measured life history parameters to determine the intrinsic rate of increase of sympatric populations of *S. punctillum* and *T. mcdanieli* over a broad temperature range, normally experienced during a growing season in southern Quebec. We also investigated if commonly used temperature-driven developmental rate models could be used to describe the relationships between temperature and r_m .

Material and methods

Rearing methods and experimental conditions

Experiments were conducted in 1994 for the spider mite and in 1995 for the coccinellid in Conviron PGR15 growth chambers (Controlled Environment Limited). *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 were maintained on red raspberry, *Rubus idaeus* L.,

cultivar Killarney at 24 °C and 50–70% relative humidity with a 16: 8 (L: D) photoperiod.

Experimental arenas consisted of 2.0 cm diameter raspberry leaf discs placed upside down on cotton wool immersed in individual 5.0 cm diameter petri dishes. The dishes were covered with lids ventilated with a 0.12 mm mesh (Nitex™). Mites and coccinellids were individually transferred to the leaf discs with a small brush. Observations were made with a stereomicroscope, provided with a cold light source.

Development and reproduction

To obtain synchronized eggs, mite and coccinellid females (ca. 100 for each species and temperature) 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 discs. Upon hatching, *S. punctillum* larvae were fed daily with excess ($\cong 300$) *T. mcdanieli* of various stages. Insects and mites were placed in growth chambers programmed for 12 constant temperature regimes: 10, 12, 14, 16, 20, 24, 28, 30, 32, 34, 36 or 38 ± 0.5 °C. The light source consisted of fluorescent lamps yielding $175 \mu \text{E s}^{-1} \text{m}^{-2}$ within each chamber, providing a 16-h daily photophase. Temperature and relative humidity in each of the growth chambers were recorded continuously with an integrated data logger. Relative humidities varied between 50 and 75%. Sixty individuals were tested per temperature regime.

Immatures were transferred on fresh leaf discs every two or three days, until mites and coccinellids matured. All individuals reaching the adult stage were observed to determine sex. Newly emerged females were isolated on fresh leaf discs and provided with a mature male throughout the oviposition period. At the onset of reproduction, females were transferred daily to fresh leaf discs and daily egg production rate was recorded throughout the adult life. For *T. mcdanieli*, eggs were collected daily, pooled within age class, and placed in petri dishes to be reared at 24 °C for secondary sex ratio determination.

Intrinsic rates of natural increase (r_m)

The r_m was estimated by non linear regression according to the Birch formula (Birch, 1948): $\sum (\exp(-r_m x) l_x m_x) = 1$ where r_m is the intrinsic rate of natural increase, x is female age, l_x is the fraction of females surviving to age x and m_x is the expected number of daughters produced per female alive at age x , obtained by multiplying number of eggs by the age-specific sex ratio for *T. mcdanieli* (Roy et al., 2002), or by 0.5 for *S. punctillum* (Chazeau, 1985).

Rate of population increase (r_m) modelling

In our previous study on modelling development rate (Roy et al., 2002), the Lactin-2 model (Lactin et al., 1995), and the Brière-1 model (Brière et al., 1999), performed best with *T. mcdanieli* and *S. punctillum*, respectively.

Substituting r_m for development rate, the Lactin (2) model is defined by the following relationship,

$$r_m(T) = e^{(\rho T)} - e^{(\rho T L - (T L - T)/\Delta T)} + \lambda$$

where T is ambient temperature; ρ is the r_m maximum which is reached at the optimal temperature; T_L is the (lethal) maximum temperature; ΔT is the temperature range over which physiological breakdown becomes the over-riding influence on r_m ; and λ forces interception with the x axis, thus allowing estimation of a low temperature threshold at which r_m falls to zero. The Brière (2) model is defined as follows,

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

where T and T_L are as above, a is an empirical constant, and T_0 is the low temperature threshold for population growth. The r_m estimates obtained at each constant temperature were used to fit these models for both species by iterative non-linear regression based on the Marquardt algorithm (TableCurve™ version 4, 1996).

Results*Age specific survival and fecundity*

Tetranychus mcdanieli successfully developed to adulthood at temperatures from 14 °C to 36 °C (Figure 1), but failed at 10 °C, 12 °C and 38 °C. The coccinellid had a narrower thermal range for reproduction than the spider mite (Figure 2). It survived to maturity from 14 °C up to 32 °C, but never reproduced at 14 °C.

The fecundity rates (m_x) of the coccinellid and the spider mite were greatly influenced by temperature (Figures 1 and 2), and the results suggest differences in age-specific temperature-dependent fecundity patterns between them. At temperatures between 14 °C and 20 °C, the m_x of *T. mcdanieli* fluctuated throughout most of the rather long oviposition period with no clearly defined peaks (Figure 1). At 24 °C and higher temperatures, m_x curves are less symmetrical, being characterized by a rapid initial increase to the maximum followed by a more gradual decrease with age. At the highest

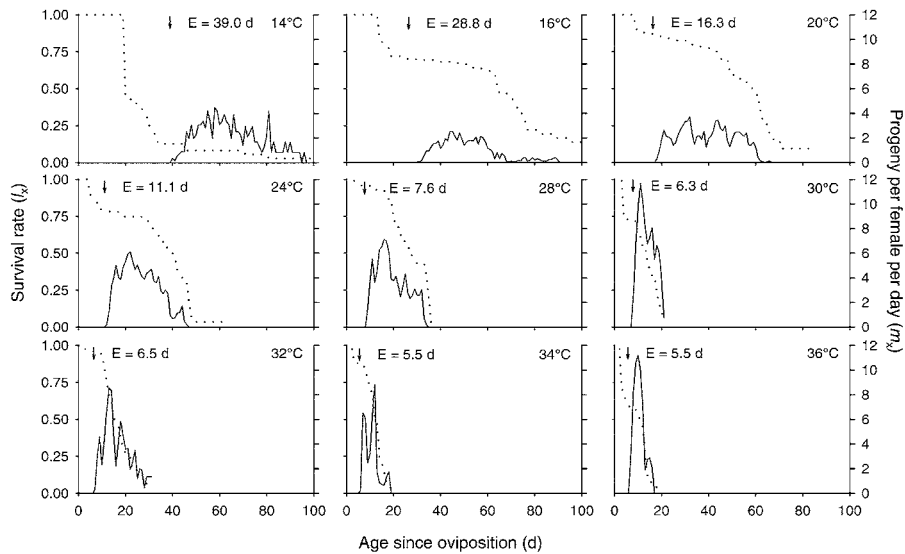


Figure 1. Age-specific survival (y axis on left, dotted line) and age-specific fecundity (y axis on right, solid line) of *Tetranychus mcDanieli* at different temperatures. The arrow indicates mean age at adult emergence (E; days).

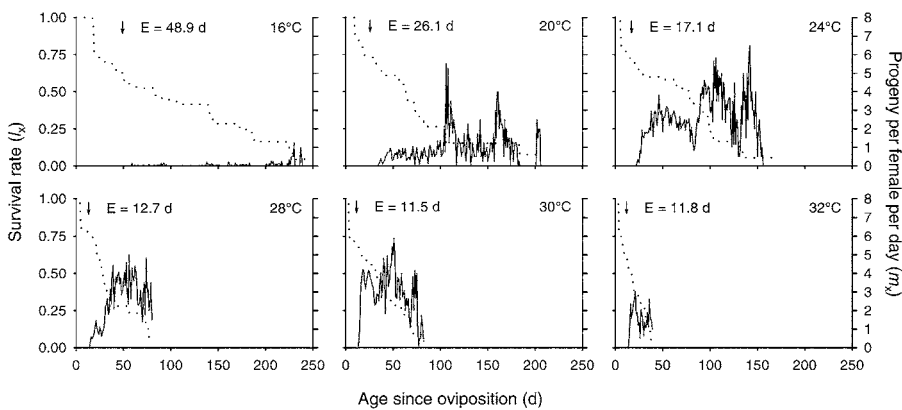


Figure 2. Age-specific survival (y axis on left, dotted line) and age-specific fecundity (y axis on right, solid line) of *Stethorus punctillum* at different temperatures. The arrow indicates age at adult emergence (E; days).

temperature (36 °C), the m_x curve was reduced to a single, well defined peak with a maximum value of 11.2 eggs female⁻¹ day⁻¹.

At 16 °C, reproduction of *S. punctillum* was sporadic and unpredictable on a short term basis. Females laid one egg occasionally during most of their reproductive life (Figure 2). At temperatures between 20 °C and 30 °C, the m_x still fluctuated greatly throughout most of the oviposition period

Table 1. Proportion of ovipositing females, duration of preoviposition and oviposition periods, longevity, and fecundity of *Tetranychus mcdanieli* at different temperatures

Temperature (°C)	n ^a	Ovipositing females (%)	Preoviposition period ^b (days)	Oviposition period ^b (days)	Female longevity ^b (days)	Female fecundity ^b (eggs)
14	8	87.5	4.0 ± 1.9	29.1 ± 12.5	36.2 ± 14.2	43.8 ± 27.3
16	30	83.3	3.7 ± 0.6	28.5 ± 12.9	35.0 ± 13.7	57.5 ± 37.2
20	41	90.2	2.2 ± 0.5	25.5 ± 15.1	28.8 ± 15.9	91.7 ± 68.9
24	32	97.0	1.2 ± 0.3	21.9 ± 9.7	24.0 ± 10.0	151.5 ± 70.9
28	39	100	1.2 ± 0.4	15.1 ± 7.5	17.0 ± 8.0	129.8 ± 58.8
30	21	100	1.0 ± 0.3	6.7 ± 3.6	7.7 ± 3.7	79.2 ± 47.2
32	47	91.5	1.1 ± 0.5	8.2 ± 5.4	9.6 ± 5.6	52.0 ± 45.3
34	35	100	0.8 ± 0.9	4.8 ± 2.7	6.1 ± 3.4	30.2 ± 18.0
36	15	100	0.8 ± 0.2	5.4 ± 2.0	6.5 ± 2.4	12.7 ± 2.3

^aNumber of females that survived to the adult stage.

^bValues are means ± standard deviation.

with egg laying occasionally decreasing, even ceasing, and resuming. For *T. mcdanieli*, maximum offspring production was observed from 20 °C to 28 °C. In contrast, maximum number of offspring produced by *S. punctillum* occurred at temperatures in the range of 24 °C to 30 °C.

Life history statistics

Stethorus punctillum longevity was 2–5 times greater than *T. mcdanieli* longevity over the range of temperature tested (Tables 1 and 2). The percentage of ovipositing *T. mcdanieli* females was greater than 83% between 14 °C and 36 °C (Table 1) with a preoviposition delay decreasing from 4.0 to 0.8 days. The oviposition periods showed a similar temperature-dependent pattern fluctuating from 29.1 days to 5.4 days. For *S. punctillum*, 52.9 and 33.3% of females that reached the adult stage at 16 °C and 20 °C, respectively, did not reproduce (Table 2). At all temperatures, the spider mites had a much shorter oviposition period than the coccinellid. For both species, oviposition usually ceased 1 to 3 days before death, except at 16 °C and 20 °C for *S. punctillum* where females stopped laying eggs 21.4 and 11.5 days, respectively, before death (data not shown).

Effect of temperature on r_m

The r_m of *T. mcdanieli* and *S. punctillum* increased almost linearly with temperature to reach a maximum and then rapidly decreased, displaying an asymmetrical dome-shaped pattern (Figure 3). Only populations of *T.*

Table 2. Proportion of ovipositing females, duration of preoviposition and oviposition periods, longevity, and female fecundity of *Stethorus punctillum* at different temperatures

Temperature (°C)	n ^a	Ovipositing females (%)	Preoviposition period ^b (days)	Oviposition period ^b (days)	Female longevity ^b (days)	Female fecundity ^b (eggs)
16	17	47.1	51.4 ± 37.4	39.4 ± 41.1	112.1 ± 40.9	6.6 ± 11.9
20	12	66.7	10.0 ± 2.1	56.0 ± 64.3	77.5 ± 60.5	69.9 ± 182.4
24	19	89.5	9.2 ± 3.2	59.9 ± 31.7	70.3 ± 35.3	279.5 ± 209.4
28	22	90.9	5.3 ± 3.3	21.1 ± 22.2	27.7 ± 23.2	110.4 ± 142.1
30	16	93.8	2.5 ± 1.0	32.4 ± 20.5	40.7 ± 19.2	231.4 ± 185.9
32	16	93.8	4.4 ± 3.5	13.0 ± 8.3	18.5 ± 8.7	46.8 ± 37.5

^aNumber of females that survived to the adult stage.

^bValues are means ± standard deviation.

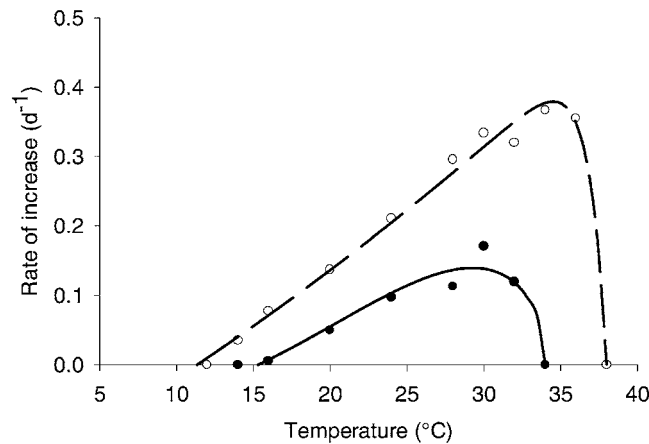


Figure 3. Intrinsic rates of increase (r_m) of *Tetranychus mcdanieli* and *Stethorus punctillum* as a function of temperature. The curves show the predicted rate using the Lactin-2 model (dashed line) for *T. mcdanieli* and the Brière-1 model (solid line) for *S. punctillum*. The dots show the observed rates (r_m).

mcdanieli could increase at 14, 34, and 36 °C. In the range 16–32 °C, suitable to both, the r_m of *T. mcdanieli* was 1.9 to 8.0 times greater than that of *S. punctillum*. *Tetranychus mcdanieli* maintained a r_m over 0.30 d⁻¹ above 28 °C, with a maximum at 34 °C, even though life-span fecundity was almost 5 times lower at 34 °C than at 24 °C (Table 1). The highest r_m of *S. punctillum* was 0.17 d⁻¹, and was recorded at 30 °C, compared to 0.36 d⁻¹ at 34 °C for *T. mcdanieli*.

The Lactin-2 model for *T. mcdanieli* and the Brière-1 model for *S. punctillum* accurately described the overall influence of temperature on r_m (Figure 3) as evidenced by the high r^2 values (0.9848 and 0.8914 respec-

tively). The r_m has a near linear relationship to temperature between 14 °C and 30 °C for *T. mcdanieli*, and between 16 °C and 24 °C for *S. punctillum*.

Discussion

In a previous study focusing on development parameters (Roy et al., 2002), we demonstrated that the range of temperatures at which *T. mcdanieli* develops to maturity (14 °C to 36 °C) is significantly larger than that for *S. punctillum* (16 °C to 34 °C). The results of the current study show a similar pattern for reproductive and survival parameters, with the range of temperatures suitable for population growth of *S. punctillum* being further reduced when compared to *T. mcdanieli*. The r_m differences observed between the predator and its prey at extreme temperatures may limit the potential of the coccinellid as a biocontrol agent of the spider mite.

The Lactin-2 and the Brière-1 models were the most useful, respectively, to predict the developmental rates of *T. mcdanieli* and *S. punctillum* as a function of temperature (Roy et al., 2002). In the present study, these models also accurately predicted their rate of increase, which is not surprising since r_m is strongly correlated to developmental rate (see e.g. Dixon, 2000, p. 168). This suggests that, even at extreme temperatures, developmental rate models could be used to obtain good fit of r_m . More attention should be devoted to identifying general conditions under which insect and mite development rate models could be used to predict their intrinsic rates of natural increase.

We used Lowess graphs (Figure 4) to examine which of the available set of temperature-dependent life-history variables may differentially influence the r_m -temperature relationship of each species. The r_m depends to a large extent on developmental rate, immature survival, fecundity and sex ratio (only for *T. mcdanieli*, a haplo-diploid with variable sex ratio; for *S. punctillum*, a constant sex ratio of 1: 1 was assumed). For *T. mcdanieli*, survival to maturity increased linearly from 16–24 °C, reaching a plateau above this range. Average progeny also increased from 16 °C to 24 °C but decreased at higher temperatures. At temperatures above 24 °C, developmental rate appears as a major contribution to rising r_m , with sex ratio, whose inverse dome-shape pattern is minimum near 24 °C, also contributing. For *S. punctillum*, immature survival and average progeny both increased up to a maximum near 24 °C, and decreased above this temperature (Figure 4). In this case, developmental rate is the only variable that continues to rise above 24 °C, slowing down the r_m inflexion and decrease due to falling survival and fecundity. Thus, in qualitative terms, differences between the r_m -temperature relationship of *S. punctillum* and *T. mcdanieli* are mainly due to their diverging survival responses: *Tetranychus mcdanieli* performs much better at high

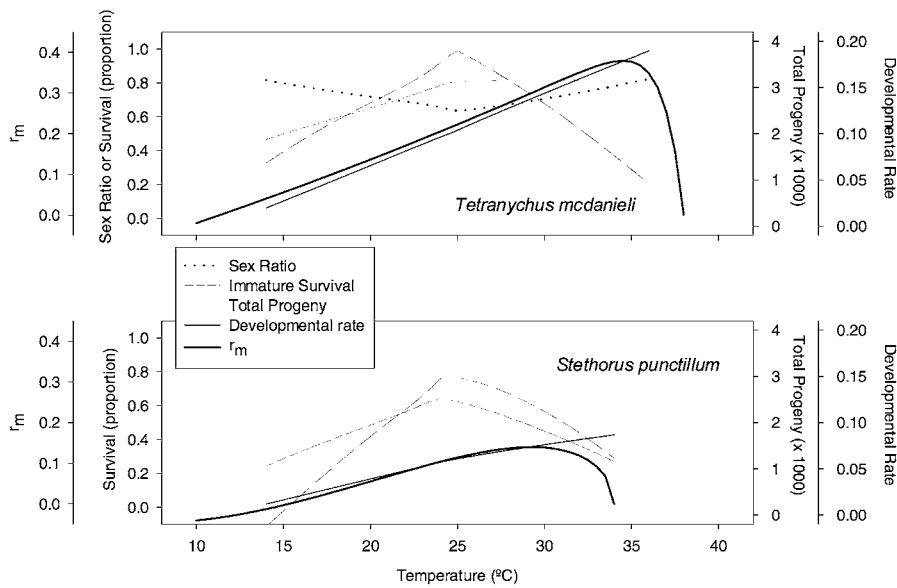


Figure 4. Lowess graphs of immature survival, developmental rate, sex ratio, total progeny per female, and r_m of *Tetranychus mcdanieli* and *Stethorus punctillum*, plotted against temperature. Sex ratio for *S. punctillum* is assumed to be 1:1.

temperature than *S. punctillum* because of a large difference in its ability to survive temperatures above 24 °C, in contrast with coccinellid survival which steadily decreases beyond that point.

Variations of the development and fecundity rates with temperature influence the r_m relation of both species in a similar, positive way (Figure 4). However, because those rates are much higher for the prey than the predator, *T. mcdanieli* displays higher intrinsic increase rate than *S. punctillum* across the whole range of overlapping temperatures favorable to both species, i.e. between 16 °C and 32 °C. In this range their r_m ratio varies from 8.0 at 16 °C to 2.7 at 32 °C, with a minimum value of 1.9 at 30 °C, in favor of the prey. The consistently higher performance of *T. mcdanieli* relative to the predator obviously results from much shorter development, and faster/earlier reproduction (Figures 1 and 2, Tables 1 and 2). Despite greater *S. punctillum* female longevity and its larger total fecundity than the prey, the population growth capacity of *T. mcdanieli* remains at least twice that of *S. punctillum*, even under the best conditions near 30 °C. However, the capacity of *S. punctillum* to track *T. mcdanieli* would be lowest in the spring at temperatures below 20 °C, and during hot summers, under temperatures exceeding 30 °C. Above this point, populations of *T. mcdanieli* could still rise, while those of *S. punctillum* would be decreasing as explained above because of rapidly

falling survival. This could partly explain the rapid build-up of spider mites populations reported in southwestern Quebec by growers in raspberry fields during summers when high temperatures prevail (Breton, 1991).

In a literature survey, Sabelis (1985a) found that the r_m of 18 colonizing species of tetranychids near 25 °C varied from 0.16 to 0.29 d⁻¹. *Tetranychus mcdanieli* ranked in the middle of the group with $r_m = 0.20$ d⁻¹ based on Tanigoshi et al. (1975), which is very close to the value obtained in the present study (0.21 d⁻¹ at 24 °C). However, estimates of r_m are difficult to compare between studies, because of genetic variation, differences in rearing methods and other environmental conditions, and variable assumptions entering these estimations. Essential life history parameters such as the sex ratio used to convert fecundity into m_x , and the rate of survival to the adult stage (Bonato, 1999) are often assumed instead of being actually measured. Tanigoshi et al. (1975) calculated r_m by assuming immature mortality to be insignificant. In our study, survival of *T. mcdanieli* to the adult stage was only 21.7% at 14 °C, and varied from 70.0 to 90.0% at temperatures of 16 °C to 36 °C (Roy et al., 2002). This variation was therefore taken into account in estimating r_m , which may partly explain differences with Tanigoshi et al. (1975). For example at 32 °C, our estimate of r_m is 0.32 d⁻¹ compared to 0.38 d⁻¹ in Tanigoshi et al. (1975), a considerable difference.

The rate of natural increase of 14 species of coccinellids specialising on different prey taxa are presented in Table 3, as measured at temperatures near 25 °C to allow direct comparison. Among acariphagous species fed spider mite prey, the r_m estimates reported for *S. loxtoni* fed *T. urticae*, *S. picipes* on *Olygonychus punicae* (Hirst) and *S. madecassus* Chazeau on *T. neocaledonicus* André, are all higher than our estimate for *S. punctillum* at 24 °C. Recently, the r_m of a chinese strain of *S. punctillum* fed on *Panonychus citri* McGregor was reported by Shen et al. (1999). In comparison, the peak r_m estimated for our Quebec strain was higher (0.17 d⁻¹) and was obtained at a higher temperature (30 °C) than for the chinese strain (0.12 d⁻¹) which peaked at 28 °C.

Dixon (2000) carefully analysed differences in life history parameters among coccinellid species specializing on aphid vs. coccid prey. He argued that coccinellids have evolved to cope with the pace of life of their specific prey. For instance, coccidophagous coccinellids tend to develop, reproduce, and age/die more slowly than aphidophagous species. As a result, aphidophagous coccinellids are characterized by larger r_m , than coccidophagous species, a difference that matches that between the r_m of their prey. Interestingly, the r_m range of acariphagous coccinellids is similar to that of aphidophagous coccinellids, being higher than coccidophagous coccinellids (Table 3). Tetranychids including *T. mcdanieli* resemble aphids more than

Table 3. Rate of natural increase (r_m) of acariphagous, aphidophagous and coccidophagous coccinellid species

Species	Prey relationship	Temp (°C)	r_m (d^{-1})	Reference
<i>Stethorus loxtoni</i> Britton and Lee	Acariphagous	25.0	0.152	Richardson, 1977
<i>Stethorus madecassus</i> Chazeau	Acariphagous	25.0	0.155	Chazeau, 1974
<i>Stethorus picipes</i> Casey	Acariphagous	24.0	0.121	Tanigoshi and McMurtry, 1977
<i>Stethorus punctillum</i> Weise	Acariphagous	24.0	0.100	Roy et al. (this study)
<i>Coccinella septempunctata</i> L.	Aphidophagous	26.0	0.190	Phoofolo and Obrycki, 1995
<i>Coleomegilla maculata lengi</i> Timberlake	Aphidophagous	25.0	0.110	Wright and Laing, 1978
<i>Olla V-nigrum</i> (Mulsant)	Aphidophagous	25.7	0.160	Chazeau et al., 1991
<i>Propylea quatuordecimpunctata</i> (L.)	Aphidophagous	26.0	0.140	Obrycki et al., 1993
<i>Diomus henneseysi</i> Furch	Coccidophagous	25.0	0.103	Kanika-Kiamfu et al., 1992
<i>Exochomus flaviventris</i> Mader	Coccidophagous	25.0	0.050	Kanika-Kiamfu et al., 1992
<i>Hyperaspis notata</i> Mulsant	Coccidophagous	25.0	0.081	Stäubli Dreyer et al., 1997
<i>Hyperaspis raynevali</i> Mulsant	Coccidophagous	25.0	0.081	Kanika-Kiamfu et al., 1992
<i>Hyperaspis senegalensis hottentotta</i> Mulsant	Coccidophagous	26.0	0.070	Fabres and Kiyindou, 1985
<i>Rodalia iceriyae</i> Janson	Coccidophagous	27.0	0.064	Kairo and Murphy, 1995

coccids in their life history strategy, with high colonizing/dispersing abilities and maximum capacity for population growth reaching 20–40% per day under favorable conditions (Wyatt and White, 1977; Sabelis, 1985a). We suggest that some acariphagous coccinellids, including *S. punctillum*, may have evolved following Dixon's model by responding adaptively to the fast pace of life of tetranychid prey, as indicated by r_m values in the 10–20% per day range under favorable conditions.

Other factors than capacity for population increase must be taken into account to predict the outcome of interactions between *T. mcdanieli* and *S. punctillum*, and their consequences to field population dynamics (Tanigoshi, 1973; Stäubli Dreyer et al., 1997; Dixon, 2000). For example, the voracious *S. loxtoni* consistently suppressed populations of *T. urticae*, yet the intrinsic rate of increase of the predator ($r_m = 0.15 d^{-1}$ at 25 °C) was less than that of its prey ($r_m = 0.17 d^{-1}$) (Richardson, 1977). A similar situation was observed by McMurtry et al. (1974) with *S. picipes* ($r_m = 0.12 d^{-1}$ at 25 °C) preying on *O. punicae* on avocados ($r_m = 0.22 d^{-1}$). The explanation could be that under highly favorable conditions, high predation rates by *Stethorus* spp. could eliminate prey more rapidly than they can reproduce. Data collected on prey consumption by *S. punctillum* during the course of this study allow

us to estimate a per capita killing rate of 75 tetranychid eggs d^{-1} for reproductive females at 20 °C. All stages of these coccinellids are known to be voracious obligate spider mite predators (McMurtry et al., 1970; Tanigoshi, 1973; Richardson, 1977). They also show strong aggregative-numerical and functional responses to prey density (Richardson, 1977; Rott and Ponsonby, 2000).

This laboratory study has shown that *S. punctillum* has a lower intrinsic rate of increase than its prey at all temperatures, and a narrower range of favorable temperature for survival, development and reproduction. Based on these observations, one might conclude that *S. punctillum* is unlikely to provide consistent control of *T. mcdanieli*, especially in cool spring and hot summer conditions. However, the short season conditions characterizing the raspberry system in Quebec imply that reproductive dynamics generally should not have a prevailing influence on predator impact. Field data indicate that *S. punctillum* colonizes raspberry only as 2nd generation adults, after several weeks of *T. mcdanieli* population growth and does not overwinter in the raspberry canopy (Roy, 2002; Roy et al., unpublished). Biological control in this system initially depends on *Amblyseius fallacis* Garman, which is well synchronized with *T. mcdanieli* in early spring, and from early summer to the end by a combination of *S. punctillum* with *A. fallacis*, both predators co-occurring at densities suggesting significant impact on spider mite densities (Roy, 2002).

Biological traits and ecological factors impacting on the efficacy of *S. punctillum* should be further investigated in order to fully evaluate its potential in raspberry. Overwintering habitat and dispersal range, searching capacity, voracity and predation rate, functional response, and interactions with other control agents, especially *A. fallacis*, are all likely to play a role in determining its potential.

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