

Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency

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Abstract Temperature is one of the most important environmental parameters influencing all the biological processes and functions of poikilothermic organisms. Although extensive research has been carried out to evaluate the effects of temperature on animal life histories and to determine the upper and lower temperature thresholds as well as the optimal temperatures for survival, development, and reproduction, few studies have investigated links between thermal window, metabolism, and trophic interactions such as predation. We developed models and conducted laboratory experiments to investigate how temperature influences predator–prey interaction strengths (i.e., functional response) using a ladybeetle larva feeding on aphid prey. As predicted by the metabolic theory of ecology, we found that handling time exponentially decreases with warming, but—in contrast with this theory—search rate follows a hump-shaped relationship with temperature. An examination of the model reveals that temperature thresholds for predation depend mainly on search rate, suggesting that predation rate is primarily determined by searching activities and secondly by prey handling. In contrast with prior studies, our model shows that per capita short-term predator–prey interaction

strengths and predator energetic efficiency (per capita feeding rate relative to metabolism) generally increase with temperature, reach an optimum, and then decrease at higher temperatures. We conclude that integrating the concept of thermal windows in short- and long-term ecological studies would lead to a better understanding of predator–prey population dynamics at thermal limits and allow better predictions of global warming effects on natural ecosystems.

Keywords Predator–prey interactions · Functional response model · Temperature window · Interaction strength · Metabolic theory of ecology

Introduction

Temperature is one of the most important environmental parameters influencing all biological process rates and functions. Temperature variations have a determinant and direct effect on ectotherm metabolism and behavior (Bale 2002), and the resulting changes in activities may have cascading effects at population and community levels (Brown et al. 2004; Hoekman 2010; Petchey et al. 2010). All organisms live within a range of temperatures allowing growth and reproduction; this is called the organism's thermal window (Dixon et al. 2009). At the upper and lower thermal limits, the organism's performance decreases due to the limiting capacity for oxygen supply and anaerobic metabolism near the critical temperatures (Portner et al. 2006; Portner and Farrell 2008). Extensive research has been carried out to evaluate the effects of temperature on animal life history and to determine the upper and lower temperature thresholds as well as the optimal temperatures for survival, development, and

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reproduction (Bale 2002; Portner et al. 2006; Dixon et al. 2009). Although it has long been recognized that different functions have different thermal windows, with active behaviors occurring in narrower windows than passive tolerance, few studies have investigated links between thermal windows and trophic interactions such as predation. This is especially relevant because temperature strongly influences interaction strengths, which have important effects on predator–prey population dynamics (Vasseur and McCann 2005) and community structure (Petchey et al. 2010).

The energetic efficiency of an organism determines the amount of energy available for activity, growth, and reproduction, thereby contributing to the organism's overall success. Energetic efficiency is the ratio between energy gain through food assimilation and energy lost through metabolism (Rall et al. 2010; Vucic-Pestic et al. 2011). According to the metabolic theory of ecology (MTE) (Brown et al. 2004), temperature is one of the most important drivers of metabolic activity and, consequently, contributes to determining predator energetic efficiency. Few studies have examined the effects of temperature on predator energetic efficiency. Vucic-Pestic et al. (2011) and Rall et al. (2010) showed that energetic efficiency decreases with warming while Vasseur and McCann (2005) found the reverse. Although the slope of this relationship remains controversial, there is now evidence that predator energetic efficiency is a major determinant of population stability (Vasseur and McCann 2005). Because predator feeding rate may vary with temperature in a nonlinear way, it is relevant to determine predator energetic efficiency across the thermal window for predation activity as suggested by Englund et al. (2011).

A simple model of predator–prey interaction strength is provided by the functional response that describes the relationship between the number of prey available and the number of prey killed by a predator (Holling 1959). Several studies on ectotherms have shown that temperature has a strong effect on functional response; typically, predation increases with warming (Thompson 1978; Gresens et al. 1982; Persson 1986; Eggleston 1990; Zamani et al. 2006). The functional response mainly depends on two behavioral parameters: search rate (the predator's searching efficiency), and handling time (the time to kill and eat a prey) (Holling 1959). Because biochemical processes of animals largely depend on temperature (Gillooly et al. 2001), both search rate and handling time are directly related to ambient temperature. Following MTE, handling time and search rate should exhibit similar temperature dependence to metabolic rate. It is predicted that search rate would increase and handling time decrease exponentially with warming (Brown et al. 2004). This exponential relationship has been well established for handling time (Mack and Smilowitz 1982; Cave and Gaylor 1989; Flinn 1991; Menon et al. 2002; Xia

et al. 2003), but remains unclear for search rate. The relationship between temperature and search rate has been described as being linear, quadratic, or hump-shaped (Mack and Smilowitz 1982; Cave and Gaylor 1989; Flinn 1991; Xia et al. 2003). Because an active behavior like searching decreases at extreme temperatures, investigating the effect over a large temperature range is necessary to draw a complete picture. Moreover, it has been recognized that variations in search rate and handling time can induce major changes in population and food-web stability (Williams and Martinez 2004; Brose et al. 2006; Rall et al. 2008). Recently, Petchey et al. (2010) developed a mechanistic model to predict the effect of temperature on food web connectance. They concluded that relative sizes of the activation energies of attack rate and handling time determine whether warming increases or decreases connectance.

Models are useful for studying the effect of temperature on predation because they can predict the functional response for any temperature–prey density combination and may help to understand the underlying mechanisms (e.g., foraging behavior). In this paper, we developed a temperature-mediated functional response model based on predator foraging behavior and following the metabolism theory of ecology. Under laboratory conditions, we investigated the potential effects of low and high temperatures on functional response, search rate, and handling time of ladybeetles feeding on aphids. Using our model, we also determined predator energetic efficiency across a large range of temperatures. The significance for population stability and community structure is briefly discussed.

Materials and methods

Biological system

We studied the functional response of a ladybeetle, *Coleomegilla maculata lengi* DeGeer (Coleoptera: Coccinellidae), preying on the green peach aphid, *Myzus persicae* Sulzer (Homoptera: Aphididae). *C. maculata*, a common natural enemy of several aphid species in North America (Benton and Crump 1981; Gordon 1985), is a good predator model to study the effect of temperature on functional response since this species has a large distribution and individuals can experience a wide range of temperatures throughout their lifetime in temperate zones.

Adult *C. maculata* (more than 4,000) were collected in October 2009 from a field in Saint-Mathieu de Beloeil (45°35'N, 74°45'W), Québec, Canada. Coccinellids were reared in sealed plastic mesh boxes (946 mL; Ziploc®), provided with moistened paper strips, and fed ad libitum with pollen, a liver-based artificial diet (Firlej et al. 2006), and aphids [*M. persicae*, *Aphis glycines* Matsumura, and

Acyrtosiphon pisum Harris (Homoptera: Aphididae)]. A colony of *M. persicae*, established from individuals collected in greenhouses from Agriculture and Agri-Food Canada, St-Jean-sur-Richelieu, Québec, Canada, was maintained on sweet pepper plants (*Capsicum annuum* L. cv. Bell Boy). Pepper plants were fertilized twice a week with Nitrophoska (12-4-14) at a concentration of 100 ppm of nitrogen (Plant-Prod, Montréal, QC, Canada). All insects and plants were reared in a growth chamber (Conviron® E15) at $24 \pm 1^\circ\text{C}$, 50–60% relative humidity, $150 \mu\text{mol} (\text{m}^2)^{-1} \text{s}^{-1}$ light intensity, and under a 16L:8D photoperiod.

Experiments

We tested the functional response of *C. maculata* at six temperatures [(mean \pm SE) 13.9 ± 0.5 , 17.6 ± 0.5 , 21.7 ± 0.3 , 25.8 ± 0.6 , 29.4 ± 0.6 , $32.8 \pm 0.9^\circ\text{C}$] and under a relative humidity of $70 \pm 8.8\%$ and a photoperiod of 16L:8D. These temperatures cover the range of temperatures allowing the complete development of *C. maculata* (Obrycki and Tauber 1978). During the experiment, temperature and humidity were recorded continuously using Hobo® U12 units. After egg hatching, *C. maculata* larvae were reared at 24°C in Petri dishes ($100 \times 15 \text{ mm}$) and fed ad libitum with green peach aphids until larvae reached the third instar. To standardize the response of tested individuals and stimulate their predatory activity, larvae were starved for 21 h in Petri dishes containing only moistened filter paper. Experimental arenas consisted of a plastic cylinder (20 cm in diameter and 45 cm in height for a surface area of $2,826 \text{ cm}^2$) glued to a plastic disc platform. The top of the cylinder and two lateral openings were covered with muslin to allow air circulation. Pepper plants used in experimental arenas were 4 weeks old with four leaves. The apex was removed because it is difficult to see aphids hidden within this plant structure. Third instar aphids (mean weight value \pm SE: $0.17 \text{ mg} \pm 0.025$) obtained from synchronous cohorts of *M. persicae* were used as prey throughout the experiment. At the onset of the experiment, aphids were transferred to the upper leaves of the plants using a fine camel hair brush. Prey densities were 5, 10, 20, 30, 45, 60, and 90 *M. persicae* per plant. Two hours after the introduction of aphids, a single newly moulted third instar *C. maculata* larva was introduced at the bottom of the stem. After 24 h, the number of remaining aphids was recorded to establish the predation rate. For each aphid density, the experiment was repeated eight times with a predator and four times without (control treatment to assess natural aphid mortality). In addition, 32 third instar *C. maculata* larvae were weighed after 21 h of starvation using a micro-balance (Mettler Toledo MT5). The mean weight value \pm SE

($4.71 \pm 2.28 \text{ mg}$) was used to parameterize the handling time equation (Eq. 4).

Statistical analyses and modeling

Data were analyzed using R (v.2.9.1; R Development Core Team, 2007). To examine the functional response of a predator, the first step is to determine the shape of the response curve. To discriminate between type II and type III functional responses, a logistic regression between the proportion of prey eaten (N_e/N_0) and initial prey density (N_0) was performed (Juliano 2001):

$$\frac{N_e}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad (1)$$

where N_e is the number of prey eaten, N_0 is the initial number of prey, and P_0 , P_1 , P_2 , and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively, estimated using the maximum likelihood method (Juliano 2001). If $P_1 > 0$ and $P_2 < 0$, the proportion of prey consumed is positively density dependent, corresponding to a type III functional response. If $P_1 < 0$, the proportion of prey consumed declines monotonically with the initial density of prey, corresponding to a type II functional response (Juliano 2001).

After determining the shape of the response curve, the parameters [handling time (day prey^{-1}) and search rate ($0.28 \text{ m}^2 \text{ day}^{-1}$; experimental arena volume/day)] were estimated using a nonlinear least-square regression procedure for the Rogers random predator equation (1972):

$$N_e = N_0 \left(1 - e^{-a(t-hN_e)} \right) \quad (2)$$

where N_e is the number of prey eaten, N_0 the initial number of prey, t the total experimental time, a the search rate ($0.28 \text{ m}^2 \text{ day}^{-1}$), and h the handling time (day prey^{-1}). Before fitting the nonlinear least-square regression, we used the package “EMDBOOK” from the R statistical software to solve the Rogers random predator equation (Bolker 2008). This yields:

$$N_e = N_0 - \frac{w(ahN_0 e^{-a(t-hN_0)})}{ah} \quad (3)$$

where w is the Lambert W function (see Bolker 2008 for details).

Based on MTE, handling time depends on body mass, M (mg), and environmental temperature, T (K):

$$h = h_0 M^{b_h} e^{E_h/kT} \quad (4)$$

where h_0 is a normalization constant independent of body size and temperature, b_h is an allometric exponent (0.75), E_h is the activation energy (eV) (defined as the average activation energy for the rate-limiting enzyme-catalyzed

biochemical reaction of metabolism), and k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$). The value of b_h is assumed to be 0.75 and is derived from the physics of distribution networks in animals (West et al. 1997); h_0 and E_h are estimated empirically using nonlinear least-square regressions.

Because preliminary results indicated a nonlinear relation between temperature and search rate, we developed a new model adapted from Briere et al. (1999) that accounts for such a nonlinear effect:

$$a(T) = \begin{cases} 0 & \text{if } T \leq T_0 \\ b(T - T_0)(T_l - T)^{1/2} & \text{if } T_0 \leq T \leq T_l \\ 0 & \text{if } T \geq T_l \end{cases} \quad (5)$$

where a is a positive function of temperature, b is an empirical constant, and T_l and T_0 are the upper and lower thresholds for search rate, respectively. This model is simple and useful for determining temperature thresholds for searching activity.

To predict the functional response over a wide range of temperatures, we developed a temperature-dependent functional response model in which handling time and search rate were substituted by Eqs. 4 and 5, respectively. These equations were modified from the Rogers random predator equation (1972) (Eq. 2):

$$N_e = N_0 \left(1 - e^{b(T-T_0)(T_l-T)^{1/2}(h_0 M^{b_h} e^{E_h/kT} N_e - t)} \right) \quad (6)$$

This model was fitted to the entire dataset using a nonlinear least-square regression procedure and the Lambert W function (Bolker 2008) to solve the recursive function of N_e .

To evaluate the energetic efficiency of *C. maculata*, we used the following equation (Vasseur and McCann 2005; Rall et al. 2010; Vucic-Pestic et al. 2011):

$$y = \frac{\omega F}{\lambda I} \quad (7)$$

where y is the dimensionless energetic efficiency of the predator, F is the per capita energy feeding rate (J h^{-1}), which is equal to the per capita biomass feeding rate (mg h^{-1}) multiplied by a weight–energy conversion factor ($1 \text{ mg wet mass} = 7 \text{ J}$ Peters 1986), ω is a temperature-independent assimilation efficiency (0.85 for carnivores; see Rall et al. 2010 for details), λ is a constant converting standard metabolic rate into field metabolic rate ($\lambda = 3$ Savage et al. 2004), and I is the standard metabolic rate. Based on MTE, we used the null model for metabolic rate (Brown et al. 2004):

$$I = i_0 M^{b_i} e^{-E_i/kT} \quad (8)$$

where i_0 is a normalization constant independent of body size and temperature (2.86×10^7 for invertebrates; Brown et al. 2004), b_i is an allometric exponent (0.75), E_i is the activation

energy for metabolism (0.65 eV; Brown et al. 2004), and k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$).

Results

Only $0.5 \pm 0.1\%$ (mean \pm SE) of the aphids died in the control treatments (without predator), and mortality did not differ among temperatures (Wilcoxon: $\chi^2 = 8.5$, $df = 5$, $P = 0.13$). As a result, we did not correct data for natural aphid mortality in our analyses.

For each temperature, the linear parameters of the logistic regression model were negative and the proportion of aphids eaten decreased when prey density increased (Fig. 1), suggesting a type II functional response at each temperature. Typically, predator voracity increased with prey density until reaching a plateau corresponding to the maximum number of prey eaten in 24 h. This number increased with temperature (Fig. 1).

Following the identification of the functional response type, the Rogers random predator equation (Eq. 3) was fitted separately for each temperature. The coefficient of determination (r^2) of the Rogers model ranged from 0.2 to 0.79, with a larger variability in predation rate at the lower temperatures (13.9, 17.6, and 21.7°C) than at the higher temperatures (25.8, 29.4, and 32.8°C), as shown in Fig. 1.

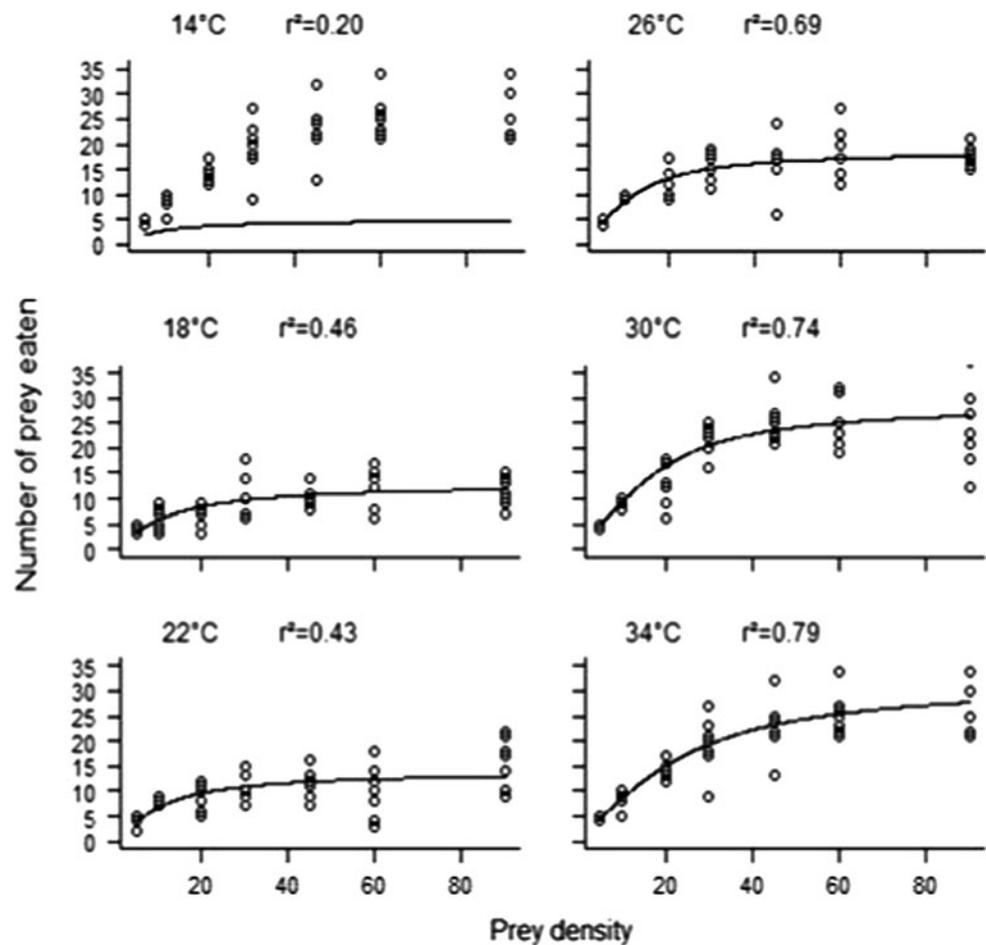
Plots of both estimated values of handling time and search rate versus temperature indicate that Eqs. 4 and 5, respectively, are appropriate for describing these two parameters (Fig. 2). As predicted by MTE, handling time decreases exponentially with warming (Fig. 2a; Table 1). In contrast, search rate increases with warming, reaches an optimum, and then decreases at higher temperatures (Fig. 2b; Table 1).

To predict the functional response of *C. maculata* feeding on *M. persicae* over a range of temperatures and to obtain better estimations of model parameter values, we fitted a temperature-mediated functional response equation (Eq. 6) to the entire dataset using nonlinear least-squares regression ($r^2 = 0.80$, $df = 329$, $P < 0.0001$, $n = 334$). Estimates and standard errors for T_0 , T_l , b , E_h , and H_0 are 285.2 ± 0.24 (K), 311.25 ± 0.31 (K), 0.11 ± 0.023 , 0.61 ± 0.038 (eV), and $9.57 \times 10^{-13} \pm 1.41 \times 10^{-13}$, respectively.

Based on model predictions, the number of prey eaten increases with increasing prey density (Fig. 3). Maximum predation increases with warming but decreases rapidly at extreme temperatures (Fig. 3). The model indicates that the lower and upper temperature thresholds for predation rate are 12.05 ± 0.24 and $38.1 \pm 0.31^\circ\text{C}$, respectively.

According to the predation rate model (Fig. 3), predator energetic efficiency increases with warming, reaches an optimum, and then decreases rapidly at higher temperatures (Fig. 4). Energetic efficiency always increases with prey

Fig. 1 Functional responses of *Coleomegilla maculata* at seven densities of *Myzus persicae* under six temperatures. The Rogers random predator equation was fitted separately for each temperature. $n = 56$ for all temperature treatments except 26 and 34°C, where $n = 55$



density, which is consistent with the classical functional response equation (Holling 1959; Rogers 1972).

Discussion

Temperature clearly influenced the magnitude of the response of *C. maculata* to *M. persicae* density (Fig. 1). As previously reported for insects, crabs, and fishes (Thompson 1978; Gresens et al. 1982; Persson 1986; Eggleston 1990; Zamani et al. 2006), the proportion of prey eaten generally increased with warming. As suggested by Rall et al. (2010) and Vucic-Pestic et al. (2011), this pattern would strengthen short-term predator–prey interactions when prey growth rate and prey density are low. Of particular interest in our study, we (1) showed that the relationship between temperature and interaction strength or predator energetic efficiency is non-linear when considering a large gradient of temperatures, (2) provided a mechanistic link between temperature and some components of predation behavior (e.g., handling time, search rate), and (3) developed a model to predict temperature

thresholds for predation activity that can be used to forecast short-term interaction strength and predator energetic efficiency across a large range of temperatures. Our study contributes towards an improved general understanding of temperature effects on predator–prey interactions by introducing the concept of thermal window into a basic model. Such a model describes the behavior of predators in a more realistic environment, i.e. across a large gradient of temperatures.

As predicted by MTE and reported in previous studies (Zamani et al. 2006; Jalali et al. 2010b), we observed an exponential decrease of handling time with warming (Fig. 2). Moreover, the estimated energy activation for handling time (0.61 ± 0.04 eV) was not different to the one predicted by metabolic theory (0.65 eV). For many predators, prey handling is driven by digestion (Jeschke et al. 2002), which depends on metabolism. This is especially true for the 24-h period of our experiment, where handling processes such as killing and ingesting prey are negligible when compared to digestion (Jeschke et al. 2002). Our results are consistent with MTE, but the difference between handling and digestion time remains to be explored.

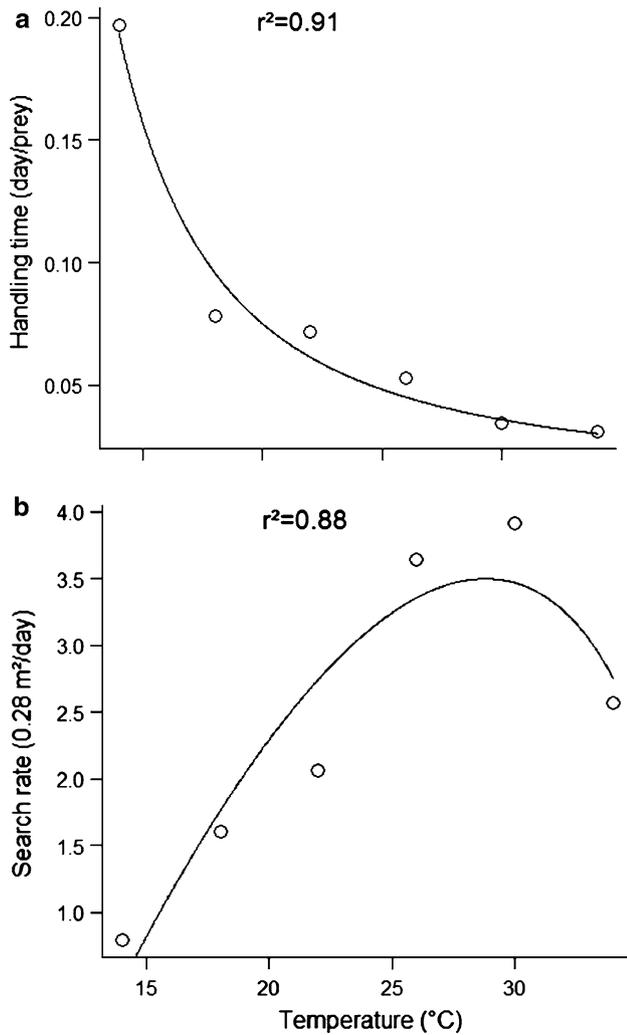


Fig. 2 Relationships between **a** temperature and handling time and **b** temperature and search rate of *C. maculata*. For handling time, $h = 8.93 \times 10^{-18} M^{0.75} e^{0.9/kT}$, where M is the predator body mass (4.71 mg), T (K) is the environmental temperature, and k is Boltzmann's constant (8.62×10^{-5} eV K^{-1}) ($r^2 = 0.91$, $P < 0.0001$, $n = 6$). For search rate, $a = 0.077(T - 285.71)(309.86 - T)^{1/2}$ ($r^2 = 0.88$, $P < 0.0001$, $n = 6$)

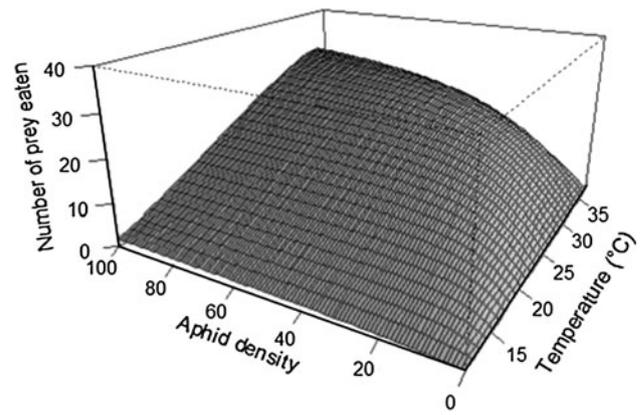


Fig. 3 Three-dimensional contour plot showing the effect of *M. persicae* density and temperature on the number of *M. persicae* eaten by *C. maculata* larvae

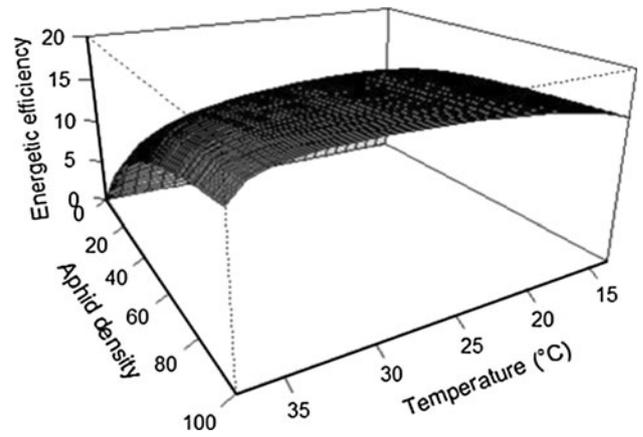


Fig. 4 Three-dimensional contour plot showing the effect of *M. persicae* density and temperature on the energetic efficiency of *C. maculata* larvae

Contrary to MTE, we found that *C. maculata* search rate follows a hump-shaped relationship with temperature (Fig. 2), indicating that foraging activity was reduced at extreme temperatures; this has been reported in prior

Table 1 Estimates of *C. maculata* search rate and handling time (mean \pm standard error and P value) using the Rogers random predator equation at six temperatures

Temperature ($^{\circ}C$)	Search rate ($0.28 \text{ m}^2 \text{ day}^{-1}$)		Handling time (day prey^{-1})	
	Mean \pm SE	P value	Mean \pm SE	P value
13.9	0.788 ± 0.367	0.0365	0.197 ± 0.023	<0.0001
17.6	1.603 ± 0.496	0.0021	0.078 ± 0.006	<0.0001
21.7	2.064 ± 0.756	0.0085	0.072 ± 0.006	<0.0001
25.8	3.638 ± 1.146	0.0025	0.053 ± 0.003	<0.0001
29.4	3.916 ± 1.293	0.0038	0.034 ± 0.003	<0.0001
32.8	2.569 ± 0.592	<0.0001	0.031 ± 0.002	<0.0001

studies (Messenger 1968; Mack and Smilowitz 1982; Cave and Gaylor 1989; Flinn 1991; Englund et al. 2011). This may result from temperature-related changes in predator metabolism: the temperature must be high enough to reach the threshold for metabolic activity, whereas temperatures that are too high reduce metabolic reaction rates through catabolism (Gillooly et al. 2001; Davis et al. 2006). Thus, the effects of increasing temperature on search rate should be different from a simple exponential relationship when a wide range of temperatures is considered. As was found in studies conducted over a small temperature range (Thompson 1978; Xia et al. 2003; Zamani et al. 2006), we found that the first section of this hump-shaped curve (lower temperatures) is well described by an exponential or linear function of temperature. However, our results suggest that search rate should be measured over a wider temperature range to include decreasing search rates at high temperatures. This decrease has an important effect on predation rate and, consequently, on the strength of trophic interactions and population stability (Persson et al. 1998; Vasseur and McCann 2005).

We developed a new model expressing handling time and search rate as functions of temperature. This model is parsimonious, provides a good estimate of *C. maculata* functional response ($r^2 = 0.80$), and can predict functional responses for any temperature–prey density combination. The model predicts that short-term interaction strengths (i.e., predation rate) increase with warming, reach an optimum, and then decrease at higher temperatures (Fig. 3). In contrast to other studies reporting an increase in predation rate with warming (Eggleston 1990; Zamani et al. 2006; Vucic-Pestic et al. 2011), we found that the effect of temperature can be nonlinear (Fig. 3). Because the decrease in predation rate occurs for temperatures close to the thermal limits (Fig. 3), a large range of temperatures should be analyzed to improve predictions for predator–prey dynamics. Our results suggest that classical functional response models such as the Holling disc (1959) or Rogers random search (1972) equations should be improved by a temperature-mediated functional response equation to produce more realistic population growth models.

Our model prediction reveals that the predator functional response is limited in a range of temperatures. Our model requires few parameters and can predict temperature thresholds for predation activity. The lower temperature threshold predicted for *C. maculata* predation activity is 12.05°C, which is consistent with field observations (Honěk 1985; Elliott et al. 2000) and laboratory observations (Giroux et al. 1995) on *C. maculata* and other aphidophagous Coccinellidae. For the upper temperature threshold, we found that predation rate is nil at 38.1°C. Very few studies have examined this threshold in coccinellids, although Soares et al. (2003) reported that the

maximum temperature for predation activity for two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) were 36.2 and 31.9°C in Petri dishes. Our model provides a reliable estimation of temperature thresholds in coccinellids and can be used to determine such thresholds for other predator–prey interactions in arthropods. An analysis of the model reveals that the upper and lower temperature thresholds depend mainly on the search rate equation. This suggests that predation rate is primarily determined by searching activities and secondly by prey handling. This should be especially true for aphidophagous predators: since aphids are patchily distributed, the first predation step is to find an aphid colony.

Dixon et al. (2005) estimated that the mean lower developmental threshold (LDT) for 22 species of Coccinellidae (including *C. maculata*) is $9.952 \pm 0.0043^\circ\text{C}$. For *C. maculata*, the estimated LDT is $11.3 \pm 0.6^\circ\text{C}$ (Obrycki and Tauber 1978). Unfortunately, upper developmental thresholds for *C. maculata* have never been estimated. Published upper developmental thresholds for aphidophagous coccinellids vary from 30 to 35°C for *A. bipunctata* and *Propylea dissecta* (Mulsant), respectively (Omkar 2004; Jalali et al. 2010a). In the present study, predation occurs between 12.05 and 38.1°C. Comparing temperature ranges for predation and for development reveals that upper and lower temperature thresholds for *C. maculata* predation are higher than those for development. The same comparison could be done for *H. axyridis* (LDT is 10.5°C, Schanderl et al. 1985; and the lower temperature threshold for activity is 12°C, Ongagna et al. 1993) and for *C. septempunctata* (LDT is 10.9–13.9°C, Obrycki et al. 1997; Xia et al. 1999; and the lower temperature threshold for locomotion is 13–15°C, Honěk 1985). This highlights the need to include dependent functional responses in dynamic population models because differences in temperature thresholds for different traits can modify predictions of dynamic population models.

As is the case for any laboratory study, our small-scale, short-term experiments have a number of drawbacks. They were conducted in an artificial environment that has little in common with the natural foraging conditions usually experienced by coccinellids in nature. For one thing, we standardized coccinellid and aphid size, but predator–prey size ratio has an important effect on predator foraging capacity (Persson et al. 1998; Vucic-Pestic et al. 2010). Other factors such as multiple prey and/or predator species interactions and experimental conditions (e.g., arena size, plant architecture, humidity) typically modify predation rates (Carter et al. 1984; Giroux et al. 1995; Xia et al. 2003). We did not consider long-term temperature effects such as thermal adaptations that should also modify the effect of temperature on metabolism and predation rate. However, we think that our approach presents a reliable

and simple mechanistic null model of temperature effects on predator–prey interactions to which additional factors may be added.

Our results suggest that predator energetic efficiency (i.e., prey ingestion relative to metabolism) depends on prey density and temperature. It increases together with prey density and reaches a maximum as predicted by the functional response equation (Fig. 4). This is to be expected since ingestion rate is directly related to predation rate, which increases with prey density. Previous studies reported that energetic efficiency can only increase (Vasseur and McCann 2005) or decrease (Rall et al. 2010; Vucic-Pestic et al. 2011) with warming. In contrast, we observed both an increase and a decrease in energetic efficiency of *C. maculata* within the temperature range we investigated (Fig. 4). At lower temperatures, the energetic efficiency increases due to a lower metabolic demand relative to the higher ingestion rate. At higher temperatures, the predator energetic efficiency decreases due to a stronger increase in the metabolic demand and a decrease in ingestion rate. Our results reveal the existence of thermal limits and optima for prey ingestion that allow for both an increase and a decrease in energetic efficiency. According to the Vasseur and McCann (2005) model, our results further suggest that population stability would decrease at lower temperatures and increase at higher temperatures. Taken together, this evidence suggests that predator–prey systems are very sensitive to temperature and that different responses can be observed depending on the intensity of warming. As suggested by other studies (Jones et al. 1998; Petchey et al. 1999; Voigt et al. 2003), higher trophic levels are more sensitive to climatic conditions, and high temperatures may induce starvation because predators would be unable to ingest sufficient food to outweigh metabolic loss (Rall et al. 2010; Vucic-Pestic et al. 2010). Such scenarios depend on predator sensitivity to temperature (Petchey et al. 1999), and our results suggest that they would vary as a function of the thermal optima for energetic efficiency.

Our study provides a simple behavioral model to predict temperature thresholds and predator functional response over a wide range of temperatures for predation activity. In contrast to MTE theory, we found that the search rate follows a hump-shaped relationship with temperature and sets the limit of predation activity. Our results further suggest that the concept of thermal windows should be applied to predator–prey interactions and population dynamics because temperature effects close to thermal limits can be different than for middle-range temperatures. Integrating the concept of thermal windows could lead to a better understanding of interaction strengths at thermal limits and of global warming effects on natural ecosystems.

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References

- Bale JS (2002) Insects and low temperatures: from molecular biology to distributions and abundance. *Philos Trans R Soc Lond B* 357:849–862
- Benton AH, Crump AJ (1981) Observations on the spring and summer behavior of the 12-spotted ladybird beetle, *Coleomegilla maculata* (Degeer) (Coleoptera: Coccinellidae). *J NY Entomol S* 89:102–108
- Bolker BM (2008) Ecological models and data in R. Princeton University Press, Princeton
- Briere J, Pracros P, Le Roux A, Pierre J (1999) A novel rate model of temperature-dependent development for arthropods. *Environ Entomol* 28:22–29
- Brose U, Williams RJ, Martinez ND (2006) Allometric scaling enhances stability in complex food webs. *Ecol Lett* 9:1228–1236
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Carter MC, Sutherland D, Dixon AFG (1984) Plant structure and the searching efficiency of coccinellid larvae. *Oecologia* 63:394–397
- Cave RD, Gaylor MJ (1989) Functional response of *Telenomus reynoldsi* [Hym.: Scelionidae] at five constant temperatures and in an artificial plant arena. *Biocontrol* 34:3–10
- Davis JA, Radcliffe EB, Ragsdale DW (2006) Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera: Aphididae). *Environ Entomol* 35:1461–1468
- Dixon AFG, Jarošik V, Honěk A (2005) Thermal requirements for development and resource partitioning in aphidophagous guilds. *Eur J Entomol* 102:407–411
- Dixon AFG, Honěk A, Keil P, Kotela MAA, Šizling AL, Jarošik V (2009) Relationship between the minimum and maximum temperature thresholds for development in insects. *Funct Ecol* 23:257–264
- Eggleston DB (1990) Behavioural mechanisms underlying variable functional responses of blue crabs, *Callinectes sapidus* feeding on juvenile oysters, *Crassostrea virginica*. *J Anim Ecol* 59:615–630
- Elliott NC, Kieckhefer RW, Beck DA (2000) Adult coccinellid activity and predation on aphids in spring cereals. *Biol Control* 17:218–226
- Englund G, Ohlund G, Hein CL, Diehl S (2011) Temperature dependence of the functional response. *Ecol Lett* 14:914–921
- Firlej A, Chouinard G, Coderre D (2006) A mericid diet for the rearing of *Hyaliodes vitripennis* (Hemiptera: Miridae), a predator of mites in apple orchards. *Biocontrol Sci Technol* 16:743–751
- Flinn PW (1991) Temperature-dependent functional response of the parasitoid *Cephalonomia waterstoni* (Gahan) (Hymenoptera: Bethyloidea) attacking rusty grain beetle larvae (Coleoptera: Cucujidae). *Environ Entomol* 20:872–876
- Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293:2248–2251
- Giroux S, Duchesne RM, Coderre D (1995) Predation of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) by *Coleomegilla maculata* (Coleoptera: Coccinellidae): comparative effectiveness of predator developmental stages and effect of temperature. *Environ Entomol* 24:748–754
- Gordon RD (1985) The coccinellidae (Coleoptera) of America north of Mexico. *J NY Entomol S* 96:1–912

- Gresens SE, Cothran ML, Thorp JH (1982) The influence of temperature on the functional response of the dragonfly *Celiithemis fasciata* (Odonata: Libellulidae). *Oecologia* 53:281–284
- Hoekman D (2010) Turning up the heat: temperature influences the relative importance of top-down and bottom-up effects in pitcher plant inquiline communities. *Ecology* 91:2819–2825
- Holling CS (1959) Some characteristics of simple types of predation and parasitism. *Can Entomol* 91:385–398
- Honěk A (1985) Activity and predation of *Coccinella septempunctata* adults in the field (Col., Coccinellidae). *Z Angew Entomol* 100:399–409
- Jalali MA, Tirry L, Arbab A, De Clercq P (2010a) Temperature-dependent development of the two-spotted ladybeetle, *Adalia bipunctata*, on the green peach aphid, *Myzus persicae*, and a factitious food under constant temperatures. *J Insect Sci* 10:1536–2442
- Jalali MA, Tirry L, De Clercq P (2010b) Effect of temperature on the functional response of *Adalia bipunctata* to *Myzus persicae*. *Biocontrol* 55:261–269
- Jeschke JM, Kopp M, Tollrian R (2002) Predator functional responses: discriminating between handling and digesting prey. *Ecol Monogr* 72:95–112
- Jones TH, Thompson LJ, Lawton JH, Bezemer TM, Bardgett RD, Blackburn TM, Bruce KD, Cannon PF, Hall GS, Hartley SE (1998) Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science* 280:441–443
- Juliano SA (2001) Nonlinear curve fitting: predation and functional response curve. In: Scheiner SM, Gurevitch J (eds) *Design and analysis of ecological experiments*. Chapman & Hall, New York, pp 178–196
- Mack TP, Smilowitz Z (1982) Using temperature-mediated functional response models to predict the impact of *Coleomegilla maculata* (DeGeer) adults and 3rd-instar larvae on green peach aphids. *Environ Entomol* 11:46–52
- Menon A, Flinn PW, Dover BA (2002) Influence of temperature on the functional response of *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae), a parasitoid of *Rhyzopertha dominica* (Coleoptera: Bostrichidae). *J Stored Prod Res* 38:463–469
- Messenger PS (1968) Bioclimatic studies of the aphid parasite *Praon exsoletum*. I. Effects of temperature on the functional response of females to varying host densities. *Can Entomol* 100:728–741
- Obrycki JJ, Tauber MJ (1978) Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasite *Perilitus coccinellae* (Hymenoptera: Braconidae). *Can Entomol* 110:407–412
- Obrycki JJ, Ormrod AM, Giles KL (1997) Partial life table analysis for larval *Coleomegilla maculata* (Degeer) and *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) in alfalfa. *J Kansas Entomol Soc* 70:339–346
- Omkar AP (2004) Temperature-dependent development and immature survival of an aphidophagous ladybeetle, *Propylea dissecta* (Mulsant). *J Appl Entomol* 128:510–514
- Ongagna P, Giuge L, Iperiti G, Ferran A (1993) Cycle de développement d'*Harmonia axyridis* (Col. Coccinellidae) dans son aire d'introduction: le Sud-Est de la France. *Biocontrol* 38:125–128
- Persson L (1986) Temperature-induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): implications for coexistence between poikilotherms. *J Anim Ecol* 55:829–839
- Persson L, Leonardsson K, de Roos AM, Gyllenberg M, Christensen B (1998) Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theor Popul Biol* 54:270–293
- Petchey OL, McPhearson PT, Casey TM, Morin PJ (1999) Environmental warming alters food web structure and ecosystem function. *Nature* 402:69–72
- Petchey OL, Brose U, Rall BC (2010) Predicting the effects of temperature on food web connectance. *Philos Trans R Soc Lond B* 365:2081–2091
- Peters RH (1986) *The ecological implications of body size*. Cambridge University Press, Cambridge
- Portner HO, Farrell AP (2008) Physiology and climate change. *Science* 322:690
- Portner HO, Bennett AF, Bozinovic F, Clarke A, Lardies MA, Lucassen M, Pelster B, Schiemer F, Stillman JH (2006) Trade-offs in thermal adaptation: the need for a molecular to ecological integration. *Physiol Biochem Zool* 79:295–313
- Rall B, Guill C, Brose U (2008) Food web connectance and predator interference dampen the paradox of enrichment. *Oikos* 117:202–213
- Rall BC, Vucic-Pestic O, Ehnes RB, Emmerson M, Brose U (2010) Temperature, predator-prey interaction strength and population stability. *Glob Change Biol* 16:2145–2157
- Rogers D (1972) Random search and insect population models. *J Anim Ecol* 41:369–383
- Savage VM, Gillooly JF, Woodruff WH, West GB, Allen AP, Enquist BJ, Brown JH (2004) The predominance of quarter power scaling in biology. *Funct Ecol* 18:257–282
- Schanderl H, Ferran A, Larroque MM (1985) Les besoins trophiques et thermiques des larves de la coccinelle *Harmonia axyridis* Pallas. *Agronomie* 5:417–421
- Soares AO, Coderre D, Schanderl H (2003) Effect of temperature and intraspecific allometry on predation by two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Environ Entomol* 32:939–944
- Thompson DJ (1978) Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. *J Anim Ecol* 47:757–767
- Vasseur DA, McCann KS (2005) A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *Am Nat* 166:184–198
- Voigt W, Perner J, Davis AJ, Eggers T, Schumacher J, Bahrmann R, Fabian B, Heinrich W, Kohler G, Lichter D (2003) Trophic levels are differentially sensitive to climate. *Ecology* 84:2444–2453
- Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: body masses constrain interaction strengths. *J Anim Ecol* 79:249–256
- Vucic-Pestic O, Ehnes RB, Rall BC, Brose U (2011) Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Glob Change Biol* 17:1301–1310
- West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126
- Williams RJ, Martinez ND (2004) Limits to trophic levels and omnivory in complex food webs: theory and data. *Am Nat* 163:458–468
- Xia JY, Van der Werf W, Rabbinge R (1999) Temperature and prey density on bionomics of *Coccinella septempunctata* (Coleoptera: Coccinellidae) feeding on *Aphis gossypii* (Homoptera: Aphididae) on cotton. *Environ Entomol* 28:307–314
- Xia JY, Rabbinge R, Van der Werf W (2003) Multistage functional responses in a ladybeetle aphid system: scaling up from the laboratory to the field. *Environ Entomol* 32:151–162
- Zamani AA, Talebi AA, Fathipour Y, Baniamiri V (2006) Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphididae), on the cotton aphid. *J Pest Sci* 79:183–188