Parsing handling time into its components: implications for responses to a temperature gradient

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Abstract. The functional response is a key element of predator–prey interactions, and variations in its parameters influence interaction strength and population dynamics. Recent studies have used the equation of the metabolic theory of ecology (MTE) to quantify the effect of temperature on the parameter Th, called "handling time," and then predict the responses of predators and communities to climate change. However, our understanding of the processes behind Th and how they vary with temperature remains limited. Using a ladybeetle–aphid system, we compared estimates of Th to direct observations of handling time across a temperature gradient. We found estimated Th values to be greater than observed Th values, suggesting that predation rate is not limited by the time available for handling prey. We next estimated the corrected digestion time, i.e., digestion time corrected for gut capacity, by subtracting observed to estimated Th values. We finally plotted the relationships between temperature and handling or digestion rates. As predicted by MTE, the corrected digestion rate increased exponentially with warming whereas, in contrast to MTE prediction, the relationship between handling rate and temperature was hump shaped. The parameter Th is thus confusing because it combines handling and digestive processes that have different thermal responses. This may explain why general patterns in the relationship between Th and temperature have been difficult to identify in previous studies.

Key words: aphid; digestion; functional response; handling time; ladybeetle; metabolic theory of ecology; predator–prey interaction; temperature.

INTRODUCTION

Understanding interactions between predators and prey is a central goal in ecology, and one significant component is the relationship between prey density and the number of prey eaten by a predator, i.e., the functional response (Holling 1959). The functional response is an essential component of most predator–prey models, and variations in its parameters influence the strength of predator–prey interactions; this has important consequences for population dynamics and food web structure (Brose et al. 2006, Petchey et al. 2008, 2010). A reliable evaluation and sound interpretation of the functional response parameters are therefore crucial to improve our understanding of the relationship between predators and prey and to identify important factors that influence the strength of this relationship.

Several models have been developed to capture the mechanistic basis of the functional response (reviewed by Jeschke et al. 2002), but the Holling's type II model,

also known as the "disk equation," remains the most popular model, probably because of its mathematical simplicity. Following Holling (1959), the number of prey eaten by the predator N_e depends on the initial number of prey N_0 as

$$N_e = \frac{aN_0t}{a\text{Th}N_0 + 1} \qquad (1)$$

where t is the total experimental time, a is the search rate (searching efficiency of the predator; units area per time), and Th is the handling time (units: time per prey). This model describes a hyperbolic curve for which the curve gradient at low prey densities is equal to a, and the asymptotic maximum under conditions of high prey densities corresponds to the reciprocal value of Th, often called the maximum intake rate.

Because the disk equation becomes invalid when a predator removes a substantial proportion of prey that are not replaced, Rogers (1972) proposed a modification of the disk equation, known as the "random predator equation," that accounts for prey depletion:

$$N_e = N_0\left(1 - e^{-a(t-\text{Th}N_e)}\right). \qquad (2)$$

Holling's and Rogers' models describe well the relationship between prey density and predation rate for most predators, but neither captures all the different

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biological processes underlying the functional response (Caldow and Furness 2001, Jeschke et al. 2002, Van Gils and Piersma 2004). While the parameter *a* (search rate) can be mechanistically explained (Holling 1966, Rogers 1972, Jeschke et al. 2002), the parameter Th represents a combination of different biological processes. In the original paper (Holling 1959), Th was described as the time needed to attack, kill, and eat a prey, and thus represents the "handling time." However, subsequent studies (see Jeschke et al. 2002 for review) have demonstrated that the parameter Th of the disc equation also includes "digestive pauses," defined as inactive periods related to digestion (Holling 1966). Typically, a predator enters into a digestive pause when satiated and resumes searching when hungry (Mills 1982, Jeschke et al. 2002). The length of the digestive pause depends on the predator gut capacity and the time needed to digest the prey (Holling 1966, Mills 1982, Jeschke et al. 2002). Because some predators handle prey faster than they digest them and vice versa, Jeschke et al. (2002) proposed that predators are limited either by their handling capacity or by their digestive capacity. Both digestion-limited and handling-limited predators have different time allocation strategies, with the latter spending more time foraging than the former (Jeschke et al. 2002, Van Gils and Piersma 2004). Because these differences have important implications for prey defense strategies and predator hunting modes (Jeschke and Tollrian 2000, Jeschke et al. 2002), it is important to identify and quantify the different processes amalgamated in parameter Th.

Temperature strongly influences parameters of the functional response, leading to important changes in predator–prey interactions, population dynamics, and food-web connectance (Vasseur and McCann 2005, Englund et al. 2011, Vucic-Pestic et al. 2011, Sentis et al. 2012). Recently, the metabolic theory of ecology (MTE) model (Brown et al. 2004) has been used to describe and predict the effect of temperature on functional response parameters (Englund et al. 2011, Vucic-Pestic et al. 2011, Rall et al. 2012, Sentis et al. 2012). According to MTE, the majority of biological rates have the same exponential temperature dependence (Brown et al. 2004):

$$I = i_0 M^{3/4} e^{-E/kT} \qquad (3)$$

where *I* is the individual metabolic rate, *M* (mg) is the body mass, *T* (K) is the environmental temperature, i_0 is a normalization constant independent of body size and temperature, *k* is Boltzmann's constant (8.62×10^{-5} eV/K), and *E* the activation energy (eV; average activation energy for the rate-limiting enzyme-catalyzed biochemical reaction of metabolism). The slope of this relationship, corresponding to the activation energy (*E*), is predicted to be 0.65 eV (Brown et al. 2004, Allen and Gillooly 2007).

Some studies have reported that the maximum intake rate (Th^{-1}) increases exponentially with warming, as predicted by MTE (Zamani et al. 2006, Jalali et al. 2010, Sentis et al. 2012), while two recent meta-analyses reported that this relationship is hump shaped, with a thermal optimum (Englund et al. 2011, Rall et al. 2012). For both meta-analyses, the authors concluded that high temperatures reduce metabolic reaction rates, suggesting that the MTE equation is not appropriate to predict the effect of temperature on maximum intake rate over large temperature ranges. In the present study, we hypothesized that this drawback originates from the nature of the handling time parameter (Th) because it combines an active behavior (handling) and a physiological process (digestion) that may have different sensitivities to temperature (Chen et al. 2003, Dell et al. 2011).

Our objectives were to (1) compare estimated values of the parameter Th to direct observations of handling time, (2) determine how the observed difference is influenced by temperature, and (3) investigate the relationships between temperature and the different components of Th (see Eq. 4). Estimates of Th were obtained from a previous functional response experiment in which third-instar *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae) larvae were exposed to eight densities of third-instar *Myzus persicae* Sulzer (Homoptera: Aphididae) (5, 10, 15, 20, 30, 45, 60, and 90) at six temperatures (14°, 18°, 22°, 26°, 30°, and 34° ± 1°C [Sentis et al. 2012]). Estimates of Th values were obtained by fitting the random predator equation (Rogers 1972) to the functional response curve (see Sentis et al. 2012). In the present study, we used video cameras to directly measure *C. maculata* handling time for *M. persicae* prey across a large temperature gradient. We next compared estimates of Th with our observations of handling time and fitted the MTE equation to the different components of Th.

MATERIALS AND METHODS

About 4000 adult *C. maculata* were collected in October 2009 in a field at Saint-Mathieu-de-Beloeil (45°35′ N, 74°45′ W), Quebec, Canada, brought back to the laboratory, and reared in sealed plastic mesh boxes (946 mL). They were fed ad libitum with pollen, a liver-based artificial diet (Firlej et al. 2006), and a mixture of aphids (*M. persicae*, *Aphis glycines* Matsumura, and *Acyrthosiphon pisum* Harris) depending on their availability in laboratory cultures. Aphid colonies were established from individuals collected in greenhouses (*M. persicae* and *A. pisum*) or fields (*A. glycines*) from the Montérégie area (Quebec, Canada). *Myzus persicae*, *A. glycines*, and *A. pisum* were maintained on sweet pepper (*Capsicum annuum* L. cv. Bell Boy), soybean (*Glycine max* L.), and broad bean (*Vicia faba* L.), respectively. All insects and plants were reared in growth chambers (Conviron E15; Controlled Environments, Winnipeg, Manitoba, Canada) at 24° ± 1°C, 50–60% relative humidity, 150 μmol·m^{-2}·s^{-1} light intensity, and under a 16L : 8D photoperiod.

Measuring C. maculata *handling time across a temperature gradient*

The experiment was conducted at six temperatures (14°, 18°, 22°, 26°, 30°, and 34° ± 1°C) and under a relative humidity of 70% ± 8%. After egg hatching, *C. maculata* larvae were reared at 24°C in Petri dishes (diameter, 100 mm; height, 15 mm) and fed ad libitum with *M. persicae* until they reached the third instar. The larvae were then isolated in Petri dishes (diameter, 40 mm; height, 12 mm) and starved for 21 h to standardize their hunger drive. At the onset of the experiment, third-instar aphids obtained from synchronous cohorts of *M. persicae* were isolated in a Petri dish (diameter, 40 mm; height, 12 mm) lined with a thin layer of agar (1.5% concentration) covered with a disk of pepper leaf (diameter, 40 mm). They were allowed to acclimatize to these conditions for 30 minutes. A single *C. maculata* larva was next introduced into the Petri dish, and its activity was recorded using an HD camera (Sony HDR-XR500; Sony, Tokyo, Japan). We viewed v\ideotapes to directly measure handling time, defined as the time interval from the beginning of an attack of *C. maculata* on *M. persicae* to the moment when the ladybeetle finished eating, i.e., end of chewing and resumption of searching behavior (walking and head swinging). In all replicates, no attack failed and *C. maculata* never walked away before entirely consuming its prey. There were 12 replicates per temperature. During the experiments, temperature and humidity were recorded continuously using Hobo U12 units (Onset Computer Corporation, Bourne, Massachusetts, USA).

Statistical analyses and estimation of Th components

For each temperature tested, a Student's *t* test was performed to determine the difference between direct observations of handling time and estimates of Th for the same temperature range obtained from Sentis et al. (2012). Because the difference was significant for each temperature, we next estimated the value of the different components of Th. According to previous studies (reviewed in Jeschke et al. 2002), the parameter Th of the disc equation can be subdivided as follows:

$$\text{Th} = t_{\text{att}} + t_{\text{eat}} + st_{\text{dig}} \tag{4}$$

where t_{att} is the attack time per prey, defined as the time between prey detection and the end of the attack; t_{eat} is the eating time per prey, defined as the time between capture and when ingestion is complete; s is the satiation per prey, defined as the reciprocal capacity of the gut (e.g., if the gut capacity of a ladybeetle is equal to 10 aphids, then $s = 0.1$); and t_{dig} is the digestion time per prey item, defined as the food transit time the gut (Jeschke et al. 2002). The sum of the first two parameters (t_{att} and t_{eat}) corresponds to the handling time as originally defined by Holling (1959), and the third term (st_{dig}) corresponds to the length of the digestive pause, i.e., the period between the end of a meal and resumption of searching. Following the terminology of

Jeschke et al. (2002), we define the length of the digestion pause as the corrected digestion time, i.e., digestion time corrected for gut capacity (st_{dig}). For each temperature tested, we estimated the corrected digestion time using

$$st_{\text{dig}} = \text{Th} - t_{\text{att}} - t_{\text{eat}}. \tag{5}$$

To examine whether the temperature response to handling rate and corrected digestion rate (st_{dig}^{-1}) deviated from the MTE model, we fitted the following quadratic model to the data (Englund et al. 2011):

$$Y = ce^{b(-1/kT) + q(-1/kT)^2} \tag{6}$$

where Y is the handling or corrected digestion rate and c, b, and q are fitted parameters. When b and q are significant and positive and negative, respectively, the quadratic model describes a concave downward (umbrella-shaped) relationship with a thermal optimum (Englund et al. 2011). In such a case, the MTE model (Eq. 3) is not appropriate to describe the temperature response (Englund et al. 2011). When b is positive and significant and q is positive or not significant, the MTE model is appropriate to describe the temperature response. In such cases, we fitted the MTE model (Eq. 3) to estimate the slope of the temperature response (parameter E). We used the mean weight of 4.71 ± 2.28 mg (mean ± SE) for third-instar *C. maculata* obtained from Sentis et al. (2012) to parameterize the MTE equation. Data were analyzed using R software, v.2.13.1 (R Development Core Team 2011).

RESULTS

Direct observations of handling time and estimates of Th both decreased with increasing temperature (Fig. 1). For each temperature tested, Th was significantly higher than the empirical observation, and this difference decreased with warming (Fig. 1). Using Eq. 5, we estimated the corrected digestion times as being 245.12, 85.94, 88.77, 64.04, 40.70, and 32.07 minutes for 14°, 18°, 22°, 26°, 30°, and 34°C, respectively.

The relationship between temperature and handling rate was hump shaped (Fig. 2a) and did not fit the MTE prediction, as indicated by a significant positive linear term b and a negative quadratic term q (Table 1). For the corrected digestion rate, the linear term b was significant and positive and the quadratic term was negative but not significant (Table 1). In such a case, the MTE model should be appropriate to describe the temperature relationship. However, because the quadratic term was negative, it is difficult to conclude definitively. As suggested by G. Englund (*personal communication*), we used the Akaike information criterion for small sample sizes (AIC$_c$) to compare the quadratic model ($R^2 = 0.92$, df = 3, $P = 0.02$) and the MTE model ($R^2 = 0.91$, df = 4, $P = 0.0033$). AIC$_c$ values (MTE model = 7.61, quadratic model = 16.37) confirmed that the MTE model better describes the relationship between temperature and corrected diges-
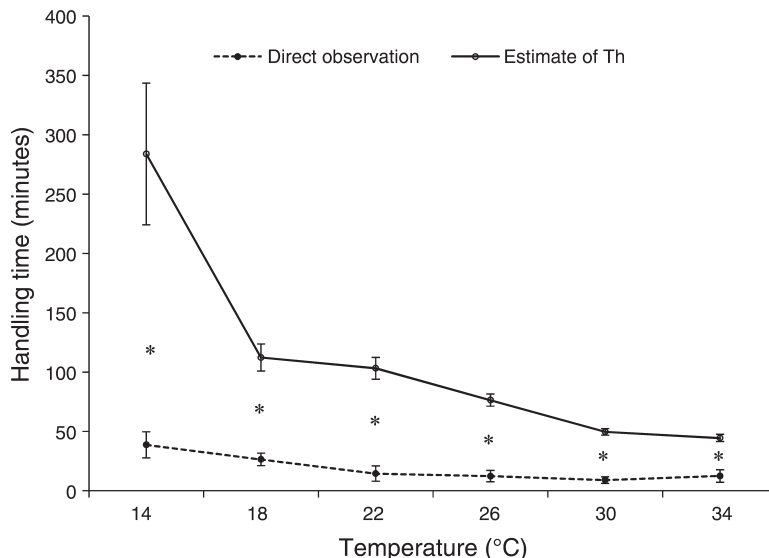
FIG. 1. Empirical observations of handling time and estimates of the handling time parameter (Th; mean ± SE) for *Coleomegilla maculata* larvae preying on *Myzus persicae* at six temperatures. For each temperature treatment, an asterisk indicates a significant difference between Th and the direct observation of handling time ($P < 0.05$).

tion rate. As predicted by MTE, the corrected digestion rate increased with warming (Fig. 2b), and the slope of this relationship is 0.69 ± 0.11 (mean ± SE).

DISCUSSION

Several studies have used the MTE equation to quantify the effect of temperature on functional response parameters and predict consequences for population dynamics and community structure (Petchey et al. 2010, Rall et al. 2010, 2012, Englund et al. 2011, Brose et al. 2012). However, our understanding of the different processes included in the parameter Th (i.e., handling time) and how they vary with temperature remains limited. When comparing estimates of Th to values obtained from direct observations of handling time across a temperature gradient, we found that estimated Th values were systematically higher, indicating that Th includes additional behaviors or processes not described in Holling's original definition. Furthermore, for each temperature tested, observed handling times were always lower than the difference between Th and observed values of handling time, suggesting that predation rate is not limited by the time available for handling prey, as is often assumed.

For each temperature tested, we estimated a corrected digestion time, which corresponds to the length of the digestive pause (Mills 1982, Jeschke et al. 2002). The corrected digestion time is directly proportional to the digestion time and thus represents a reliable estimate of the latter (Jeschke et al. 2002). Because of the difficulty of analyzing gut content, especially for small arthropods, very few quantitative data are available for gut capacity and digestion time of insects. However, PCR-based gut content analysis in ladybeetles revealed that

prey DNA detection time, an indirect measure of digestion time, varied from 1 to 19 h depending on the predator species and prey species and size (Hoogen-doorn and Heimpel 2001, McMillan et al. 2007, Gagnon et al. 2011). Our estimates of the corrected digestion
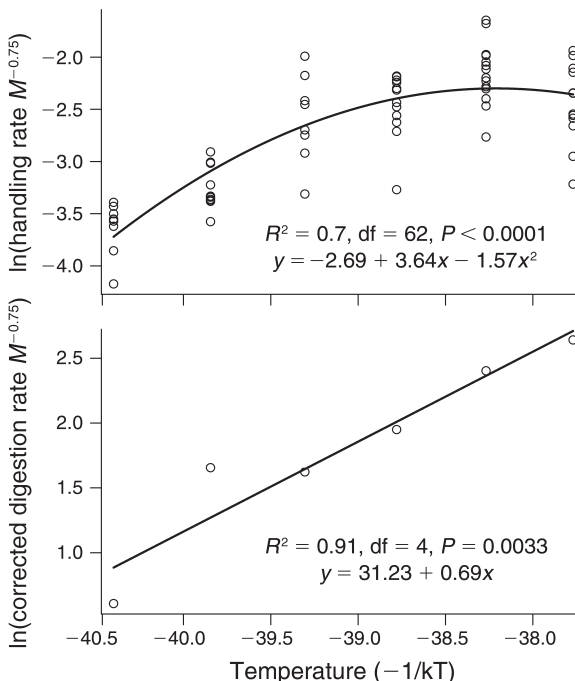

FIG. 2. The relationships between (A) handling and (B) corrected digestion rates and inverse temperature (T, Kelvin) scaled with the Boltzmann constant (k) for *Coleomegilla maculata* larvae preying on *Myzus persicae*. M represents the mean mass of third-instar *C. maculata* (4.71 mg).

TABLE 1. Parameter values (mean $\pm$ SE and P value) for the temperature dependence of handling and corrected digestion rates for *Coleomegilla maculata* larvae preying on *Myzus persicae* estimated from the quadratic model (Eq. 6).

Parameter	Handling rate		Corrected digestion rate	
	Mean $\pm$ SE	P	Mean $\pm$ SE	P
c	-2.69 ± 0.04	<0.0001	2.98 ± 0.10	<0.0001
b	3.64 ± 0.33	<0.0001	1.53 ± 0.25	0.009
q	-1.57 ± 0.33	<0.0001	-0.21 ± 0.25	0.47

time vary from 0.5 to 4 h at 34° and 14°C, respectively, and fit within the range of values reported for coccinellids. This supports the idea that the digestion process contributes to explaining the differences between estimated Th and observed handling time. Furthermore, other non-predatory activities, such as interactions between predators (e.g., interference competition), reproductive activities (e.g., mating, oviposition), and developmental processes (e.g., molting), can also reduce the time available for predation. However, to minimize the confounding effect of non-predatory activities, third-instar coccinellid larvae were isolated to prevent intraspecific interactions and age-standardized to avoid molting during our experiment. Thus digestion is likely the main process accounting for differences between Th and the observed handling time.

Handling time is often identified as the limiting factor for predation rate because the reciprocal value of Th corresponds to the maximum feeding rate at high prey densities. However, handling time values for *C. maculata* were always lower than the length of the digestive pause (i.e., corrected digestion time), suggesting that digestion is the main limiting factor of predation rate in this system. This result may not be an exception, since most predators handle prey faster than they digest them (Jeschke et al. 2002). Predators have evolved different life history and predation strategies depending on the factors that limit predation rate: handling-limited predators spend almost all of their time foraging whereas digestion-limited predators spend a large part of their time budget resting when satiated and digesting (Jeschke et al. 2002). These differences may have important implications for predator and prey life history traits, such as prey defense strategies or predator digestive capacity (Jeschke and Tollrian 2000, Jeschke et al. 2002). Because the parameter Th combines digestion and handling processes, it is not possible to determine which process limits predation rate when using the disk equation. Therefore, parameters of the disk equation, especially Th, should be interpreted cautiously because they may lead to erroneous conclusions about the ecology of predators and the factors governing predator–prey interactions (Jeschke et al. 2002).

As predicted by MTE and reported in previous studies (Chen et al. 2003, Dell et al. 2011), we observed an exponential increase in the corrected digestion rate with temperature (Fig. 2). Moreover, the estimated activation

energy (0.69 $\pm$ 0.11 eV) was very close to the MTE prediction (0.65 eV; Allen and Gillooly 2007). In contrast to MTE, the relationship between handling rate and temperature was hump shaped (Fig. 2), indicating that handling activity was reduced at extreme temperatures; this has been reported in other studies (Englund et al. 2011, Rall et al. 2012). We postulate that the parameter Th is confusing because it includes two processes that have different responses to temperature. Its sensitivity to temperature then depends on the relative importance of digestion and handling processes. In line with our results, a recent meta-analysis by Dell et al. (2011) revealed that internal processes such as digestion rate have lower thermal sensitivities than positive somatic traits such as foraging or handling rates. Moreover, active behaviors, such as hunting, occur in narrower thermal windows than physiological processes (Chen et al. 2003, Dell et al. 2011, Huey and Kingsolver 2011). Altogether, this suggests that the MTE model will fit digestion-limited predators well because Th is mainly driven by digestion time. This would not be the case for handling-limited predators because Th is mainly driven by the handling capacity of predators, which, in contrast to MTE prediction, decreases at high temperatures (Fig. 2). This may explain why some studies observed an exponential increase of the maximum feeding rate (Th^{-1}) with warming while Englund et al. (2011) reported that this relationship is hump shaped with an optimal value. We conclude that handling and digestion should be treated as two different features in future studies to improve our understanding of the relationship between temperature and important features of predator–prey interactions such as handling and digestion.

Because the parameter Th limits predation rate at high prey densities, it greatly influences predator–prey interaction strengths and has consequences for population dynamics, community structure, and food-web stability (McCann et al. 1998, Rall et al. 2008, 2010). For instance, Petchey et al. (2010) demonstrated that the relative thermal sensitivity of attack rate and Th determine whether warming increases or decreases connectance. Our study reveals the need to identify the basic components of species' interactions and to investigate how warming might affect these key mechanisms in order to gain knowledge on how communities might respond to climate change. Our results suggest that the effects of global warming on trophic interac-

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tions not only depend on the foraging capacity of predators but also on their digestive capacity. This highlights the need to link physiological and behavioral models in future studies.

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