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Developmental and reproductive responses of the spruce budworm (Lepidoptera: Tortricidae) parasitoid *Tranosema rostrale* (Hymenoptera: Ichneumonidae) to temperature

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ABSTRACT

The temperature-dependent development and survival of immatures, as well as adult longevity and potential fecundity of the endoparasitoid *Tranosema rostrale* (Hymenoptera: Ichneumonidae) parasitizing spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae) larvae was investigated under laboratory conditions at several constant temperatures ranging from 5 to 30 °C. Maximum likelihood modeling approaches were used to estimate thermal responses in development, survival, and longevity. A model describing the effect of temperature on potential fecundity of the parasitoid was also developed taking oogenesis and oosorption into account. In-host and pupal development rates of the parasitoid increased with temperature up to 25 °C, and decreased thereafter. Immature survival was highest below 20 °C, and rapidly decreased at higher temperatures. Adult longevity decreased exponentially with increasing temperature for both males and females. Highest potential fecundity was reached at 10 °C. Considering survival and potential fecundity, the parasitoid seems best adapted to cool temperatures below 20 °C. Simulations of the life-history traits under variable temperature regimes indicate that temperature fluctuations decrease survival and increase realised fecundity compared to constant temperatures. The temperature-dependent fecundity model developed can be applied to other non-host-feeding synovigenic parasitoids. The equations and parameter estimates provided in this paper can be used to build comprehensive models predicting the seasonal phenology of this parasitoid and spruce budworm parasitism under changing climatic conditions.

1. Introduction

Insects are poikilotherms, and as such their metabolic, survival, developmental, and reproductive rates all depend on ambient temperature (Régnière and Powell, 2013). Knowledge of the influence of temperature on insects is therefore crucial to understanding changes in seasonal patterns of phenology (Powell and Logan, 2005), distribution (Régnière et al., 2012a), as well as overall population dynamics (Kingsolver, 1989; Gray, 2008). Temperature can also affect interactions between insects at different trophic levels and can alter the dynamics of their populations (Fleming and Volney, 1995; Gray, 2008; Hance et al., 2007).

In the context of climate change, and especially climate warming predictions, the study of temperature impacts on insects has gained particular attention (e.g. reviewed by Bale et al., 2002; Deutsch et al., 2008; Kingsolver et al., 2013). Higher trophic levels, such as natural enemies of insect herbivores, are predicted to be more sensitive to a changing climate because they often have relatively narrow host ranges and depend on the capacity of their hosts and lower trophic levels to adapt to the changes (Hance et al., 2007; Harvey, 2015). Increasing temperature and extreme weather events such as heat waves are known to affect parasitoids in many ways (Hance et al., 2007). While research on insect responses to climate change for some taxa is relatively abundant (e.g. Lepidoptera), there is less information on Hymenoptera (Andrew et al., 2013), the insect order most parasitoids belong to. However, it is important to not only study the effect of climate warming at the species level, but also in the context of insect communities over several trophic levels (Harvey, 2015). To do so, basic information on the effect of temperature on key life-history traits of all trophic levels is needed to better predict impacts on insect communities by using ecological modeling approaches.

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Temperature can affect not only parasitoid development time, survival, and longevity, but also their fecundity, a determinant of the number of hosts they can potentially attack (Lysyk, 1998; Sagarra et al., 2000; Ris et al., 2004). Two general reproductive strategies can be distinguished in female parasitoids: pro-ovigeny, where females emerge with their full lifetime egg complement, and synovigeny, where adult females emerge with only a few, if any, mature eggs and develop more during their life (Flanders, 1950). There is evidence that species rank along a continuum of these strategies, ranging from purely pro-ovigenic to purely synovigenic strategies (Jervis et al., 2001). Some synovigenic parasitoids have evolved two concurrent physiological processes that determine their fecundity: egg production (oogenesis) and egg resorption (oosorption) (Jervis et al., 2001). The current understanding of egg resorption is that it acts as a buffer against environmental stochasticity (Richard and Casas, 2009) by allowing the female to regain energy from her own eggs for important metabolic processes (Bell and Bohm, 1975), and therefore to invest in future rather than immediate fitness. In insects, both egg maturation (Papaj, 2000) and egg resorption (Bell and Bohm, 1975; Barbosa and Frongillo, 1979; Santolamazza-Carbone et al., 2008) are temperature-dependent processes.

The spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), is a major pest insect that is native to North America. It undergoes periodic outbreaks at irregular intervals, averaging 35–40 years, in boreal coniferous forests across eastern North America (Blais, 1965; Morin, 1994), where it causes defoliation and mortality of balsam fir *Abies balsamea* (L.) Miller, and, to a lesser extent, several spruce species including white, *Picea glauca* (Moench) Voss; red, *P. rubens* Sarg; and black, *P. mariana* (Miller) BSP (MacLean, 1980). Parasitoids are prominent among the several factors that influence spruce budworm population dynamics (Royama, 1984; Régnière and Lysyk, 1995; Régnière and Nealis, 2007). The parasitoid community of the spruce budworm changes depending on its host's density (Eveleigh et al., 2007), and at low population density parasitoids are the main mortality factor (Régnière et al., 2013).

The koinobiont (allows the hosts to continue development and remain mobile after parasitization) synovigenic larval endoparasitoid *Tranosema rostrale* (Brischke) (Hymenoptera: Ichneumonidae) is a key mortality factor in low-density spruce budworm populations in Québec, Canada, where it can inflict mortality rates >90% (Cusson et al., 1998; Seehausen et al., 2013, 2014). Little is known about *T. rostrale*'s seasonal history despite its importance in the dynamics of spruce budworm populations during the period between outbreaks. Attacks on spruce budworm start in late May during the third and fourth instars (Cusson et al., 1998; Seehausen et al., 2016a). Although the actual duration of the parasitoid's larval and pupal development in the field is unknown, the larva emerges from its host within a few weeks of oviposition, mainly when the host larva is in the fifth or sixth instar, and forms a silk cocoon on the foliage near the host's cadaver (Cusson et al., 1998). Adults emerge from the cocoon in early July, and it is believed that the parasitoid has more than one generation per year in the locations where it has been studied in central Québec (Cusson et al., 1998). Nothing is known of its overwintering habitat or life stage.

As a first step in addressing these knowledge gaps, we obtained basic information on *T. rostrale*'s developmental, survival, and reproductive responses to temperature. To this end, the parasitoid was reared in growth chambers at constant temperatures between 5 and 30 °C, and the non-linear thermal responses of development and survival of immature stages, and longevity and potential fecundity of adults were described. The results constitute foundational information that will be eventually used to develop a seasonal biology model for this species.

2. Material and methods

2.1. Insect collection

Adult *T. rostrale* were obtained by exposing laboratory-reared third- to sixth-instar spruce budworm larvae to parasitoids on balsam fir trees in two study sites in Québec, near Armagh (46°46′ N, 70°39′ W, 312 m) and Petit lac à l'Épaule (47°18′ N, 71°12′ W, 725 m) (Lethiecq and Régnière, 1988), where parasitism rates by *T. rostrale* have been consistently high over the last 25 years (J.R., unpublished data). Different instars were exposed in the field according to their natural time of occurrence, as determined by the Spruce Budworm Seasonal Biology Model (Régnière et al., 2012a). Host larvae were recovered after 1 week in the field and reared either on an artificial diet (McMorran, 1965) or on balsam fir foliage at room temperature until parasitoid or moth emergence. Adult parasitoids were identified using dichotomous keys (Cusson et al., 1998; Bennett, 2008).

2.2. Stage-specific development time and survival

Spruce budworm larvae were reared under laboratory conditions on balsam fir foliage and fifth instars were parasitized by *T. rostrale* as described by Seehausen et al. (2016b). This host instar was chosen because of its convenient size and development time. Survival and development time of *T. rostrale* does not differ between spruce budworm instars (Seehausen et al., 2016a). Immediately after parasitism, larvae were transferred into 237-ml transparent plastic containers with screened windows for ventilation and a twig of balsam fir foliage with at least three current-year shoots that were inserted into a glass vial with water. Within 1 h of parasitism, a total of 212 parasitized spruce budworm larvae were transferred into growth chambers set at 11 constant nominal temperatures, 5, 7.5, 10, 12.5, 15, 17.5, 20, 22.5, 25, 27.5 and 30 °C (14–26 larvae per temperature). Balsam fir foliage was renewed every 1–7 days, depending on rearing temperature, until parasitoid or moth emergence. Parasitoid sex was determined at emergence by the presence or absence of the ovipositor. The temperature transfer method (Régnière et al., 2012b) was used to rear *T. rostrale* in-host (eggs and larvae) and pupae at the more extreme temperatures. At low temperature, insects were alternately kept at 5 and 7.5 °C for 5 days and at 15 °C for 2 days, until completion of the life stage. At high temperature, insects were alternately placed at 27.5 and 30 °C for 2 days then at 15 °C for 5 days. For all parasitoids, stage- (in-host or pupa) and sex-specific development time and stage-specific survival were recorded on a daily basis. Parasitized spruce budworm larvae dying from causes other than parasitoid egression were noted and excluded from the analysis of development time and survival.

2.3. Adult longevity

Adult parasitoids (64 females and 65 males) were transferred <24 h after emergence into the above described 237-ml transparent plastic containers and placed into growth chambers at six constant nominal temperatures: 5, 10, 15, 20, 25 and 30 °C. Instead of branches, the glass vials at the bottom of the container held cotton rolls soaked with a 20% sucrose water solution. Insects were provided *ad libitum* with the solution that was renewed every 1–4 days, depending on rearing temperature. All insects were observed daily and the day of death was recorded for each individual.

2.4. Potential fecundity

A total of 269 virgin parasitoid females were transferred within 24 h of emergence into transparent plastic cages with a 20% sucrose water solution as described above. Subsequently, cages were randomly assigned to one of six growth chambers at 5, 10, 15, 20, 25 and 30 °C. At all temperatures, about 10 females were dissected in a saline buffer solution under a binocular microscope after 5, 10, 15 and 20 days to count all eggs in the oviducts. Detailed methods for counting eggs in *T. rostrale* oviducts are described by Seehausen et al. (2016b). Additional females were dissected after 3 and 7 days at 20, 25 and 30 °C (again about 10 females at all temperatures). At 30 °C, no females survived beyond 20 days.

Temperature and humidity in all growth chambers were measured every 5 min with HOBO® data loggers (ONSET, U12-012). Mean relative humidity in the growth chambers was 73, 76, 89, 79, 82, 75, 71, 50, 64, 40 and 59% at 5, 7.5, 10, 12.5, 15, 17.5, 20, 22.5, 25, 27.5 and 30 °C, respectively. Because the temperature in the growth chambers fluctuated slightly (±2 °C) during the experiments, stage-specific (in-host, pupa, and adult) mean temperatures experienced by each individual were calculated and used in the analyses.

2.5. Data analysis

2.5.1. Stage-specific development time

The developmental response of immature stages (eggs and larvae inside the host and pupae after egression) was described with the model of Sharpe and DeMichele (1977), as modified by Schoolfield et al. (1981). Parameters of this model refer to the thermodynamics of enzyme reactions, assuming the rate of the modeled process is controlled by a single enzyme:

$$r = \frac{(\rho + \rho_m)\frac{K}{298}\exp\left[\frac{H_A}{R}\left(\frac{1}{298}-\frac{1}{K}\right)\right]}{1+\exp\left[\frac{H_L}{R}\left(\frac{1}{T_L}-\frac{1}{K}\right)\right]+\exp\left[\frac{H_H}{R}\left(\frac{1}{T_H}-\frac{1}{K}\right)\right]}\varepsilon \quad \text{for } K > 273, \qquad (1)$$

where K is temperature in °Kelvin, $R = 1.987 \times 10^{-3}$ kcal K^{-1} mol^{-1} is the universal gas constant, ρ is the development rate at 25 °C (298°K), H_A is the enthalpy of reaction activation (kcal mol^{-1}), T_L is the low temperature at which the 50% of the rate-controlling is inactive (°K), H_L is the change in enthalpy associated with low-temperature inactivation (kcal mol^{-1}), T_H is the high temperature at which 50% of the rate-controlling enzyme is inactive (°K), H_H is the change in enthalpy associated with high temperature inactivation (kcal mol^{-1}), and ε is a unit-less lognormal random variable with mean = 1 and variance = σ_ε^2.

The set of parameters $\{\rho, \rho_m, H_A, H_L, T_L, H_H, T_H, \sigma_\varepsilon^2\}$ was estimated for each life stage, with ρ_m being the male differences with females. Eq. (1) was fitted to individual sex-specific development times, some including transfer treatments, using the method described by Régnière et al. (2012b) with SAS (PROC NLMIXED; SAS Institute Inc., 2015).

2.5.2. Stage-specific survival

Stage-specific survival (number of specimens surviving relative to number of specimens starting the life stage) was analyzed as suggested by Régnière et al. (2012b), using logistic regression with the binomial distribution (PROC NLMIXED; SAS Institute Inc., 2015). The approach assumes that survival s during the given life stage is dependent on temperature T and exposure time t and is given by:

$$s = \left[1+e^{(-\beta_0+\beta_1 T_1+\beta_2 T_1^2)}\right]^{-t_1}\left[1+e^{-(\beta_0+\beta_1 T_2+\beta_2 T_2^2)}\right]^{-t_2}, \qquad (2)$$

where T_1 and T_2 are the two temperatures involved in transfer treatments, lasting a total of t_1 and t_2 days, respectively, and $\{\beta_0, \beta_1, \beta_2\}$ are parameters to be estimated. For temperature treatments not involving transfers, t_2 is set to 0. This logistic model was fitted by adding terms one at a time until further addition did not reduce the AICC. Using the resulting significant parameters, the life-stage's daily survival function is then:

$$s_d(T) = \left[1+e^{-(\beta_0+\beta_1 T+\beta_2 T^2)}\right]^{-1}, \qquad (3)$$

from which the stage-specific survival function was calculated over the duration of the life stage:

$$s(T) = \left[1+e^{-(\beta_0+\beta_1 T+\beta_2 T^2)}\right]^{-1/r(T)}, \qquad (4)$$

where $r(T)$ is the development rate of the life stage at temperature T as provided by Eq. (1). In the case of in-host survival, the right-hand side of Eqs. (2)–(4) was multiplied by 0.828 to adjust for pseudo-parasitism (no oviposition during an attack of the host), as determined by Seehausen et al. (2016b).

2.5.3. Longevity

Adult longevity and the ageing rate of males and females were analyzed using the same maximum likelihood approach based on individual development times. Longevity l was described as a function of temperature T with:

$$l = \left[e^{a+a_m}\left(e^T\right)^{b+b_m}\right]^{-1}\varepsilon, \qquad (5)$$

where a and b are parameters for females, a_m and b_m are differences of these parameters to describe male longevity, and ε is a lognormal random variable with mean = 1 and variance = σ_ε^2, also a parameter to be estimated.

2.5.4. Potential fecundity

To analyze the potential fecundity data, we posited that egg production P resulted from two simultaneous and opposite processes (King and Richards, 1968; Richard and Casas, 2009) in adult females of *T. rostrale*: oogenesis O and egg resorption R. We further postulated that resorption is not perfectly efficient at returning energy to the female for further egg production, through a constant κ that represents the loss of energy associated with egg resorption. Thus, in discrete difference-equation notation we define egg production as:

$$P_t = P_{t-\Delta t} + O_t - \kappa R_t. \qquad (6)$$

The rate of oogenesis (O_t) depends directly on temperature T (°C, with intercept and slope parameters a, b), is inversely proportional to the number of eggs already produced ($P_{t-\Delta t}$) relative to some maximum egg production P_{max}, and is always $\geqslant 0$:

$$O_t = \max\left[\frac{P_{\max} - P_{t-\Delta t}}{P_{\max}}(a+bT),\ 0\right]. \qquad (7)$$

This formulation produces the typical diminishing-return (asymptotic) behaviour of egg accumulation, and suggests that as energy reserves are exhausted, the production of new eggs slows down.

The rate of resorption is also directly dependent on temperature (with intercept and slope parameters c, d), is directly proportional to the number of eggs already produced, and is also $\geqslant 0$:

$$R_t = \max\left[\frac{P_{t-\Delta t}}{P_{\max}}(c+dT),\ 0\right]. \qquad (8)$$

This equation illustrates the concept that when energy reserves are high, there is little resorption, but as they drop, resorption increases.

In the absence of oviposition, eggs in the oviducts E accumulate according to:

$$E_t = E_{t-\Delta t} + O_t - R_t, \quad (9)$$

with initial condition E_0, i.e. the average number of eggs contained in the oviducts of females at emergence. This value was estimated by dissecting emerging females, with $E_0 = 9.1 \pm 1.4$ SEM eggs/female (n = 17; Seehausen et al., 2016b). The distribution of this number is near-lognormal, with mean = 1.97 and standard deviation = 0.8 (Anderson-Darling = 0.49, P = 0.19, n = 17). In Eq. (9), the inefficiency parameter is not used because we are describing the number of eggs, not the energy they represent.

When a female is allowed to lay all her eggs, the oviposition rate (eggs per day) is simply:

$$\mathrm{Ovi}_t = O_t - R_t \quad (10)$$

Because of the iterative nature of the fecundity model (discrete difference equations), parameters were estimated using Microsoft Excel's Solver, minimizing the residual sum of squares (maximizing R^2) between observations and simulation output on corresponding days at corresponding nominal temperatures. By trial and error, we also estimated the amount of variation in the value of P_{max} among individuals ($\sigma_{P_{max}}$) by comparing the observed standard deviation of mean number of eggs in females with the width of the bands of predicted egg accumulation produced for females emerging, $E_0 = \bar{E}_0 \pm \sigma_{E_0}$ and $P_{\max} = \bar{P}_{\max} \pm \sigma_{P_{\max}}$.

2.5.5. Simulation of survival and fecundity at constant and variable temperature

We ran simulations of stage-specific survival and fecundity of the parasitoid under various temperature regimes to investigate the behaviour of our models and the effect of constant and variable temperature on its output. For simulations at variable daily temperature, we generated normally-distributed temperature time-series with means of 5–30 °C in steps of 1 °C and a standard deviation of 5 °C ($\sigma = 5$). We then calculated (a) expected in-host and pupal survival of average individuals (i.e. using mean parameter estimates) during their development, and (b) egg production, accumulation in non-ovipositing females, and oviposition in females laying all available eggs, again for the average individual ($E_0 = 9.1$ and $P_{max} = 143$) during its expected lifetime. All simulations were conducted on a daily time step.

3. Results

3.1. Stage-specific development time

The unimodal nature of the thermal response of in-host and pupal development time was clearly displayed in our data, with the shortest development times of approximately 11 days inside the host and 9 days in the pupal stage occurring at about 25 °C (Fig. 1). Above 25 °C, development time rapidly increased again, and the development rate dropped to near-zero at about 35 °C. Sex had no effect on in-host development, but male pupae developed about 10% faster than females at all temperatures

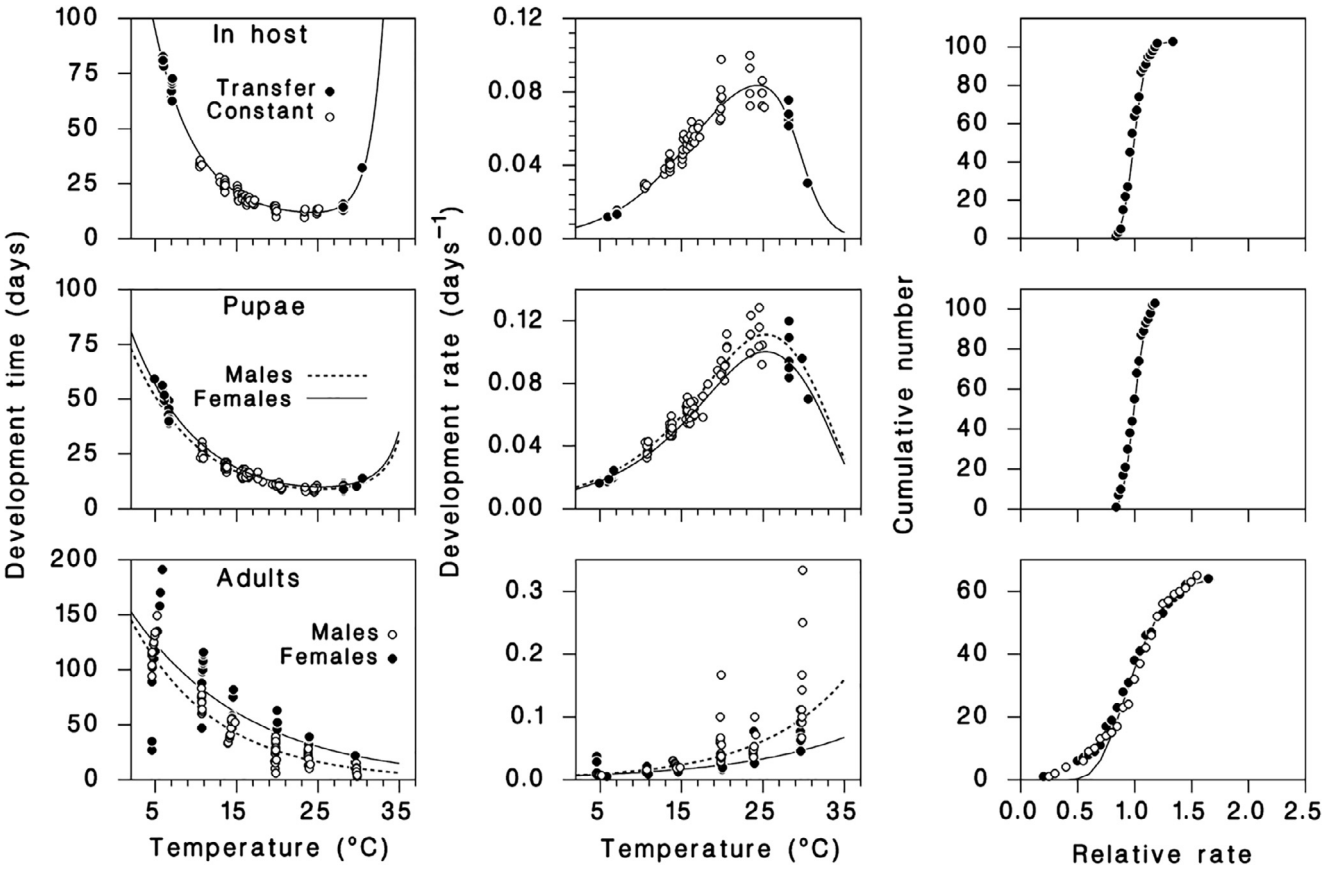

Fig. 1. *Tranosema rostrale* development and longevity data fitted to Eqs. (1) and (5). Left column: development time; middle column: development rate; right column: distribution of individual variation with the corresponding lognormal distribution. In-host (egg and larva; upper row) and pupal (middle row) development for males (dotted line) and females (solid line) at constant temperature (open circles) and temperature transfer treatments (closed circles); and adult longevity and ageing rate (bottom row) for males (open circles) and females (closed circles).

Table 1
Parameter estimates for *Tranosema rostrale*'s temperature-dependent in-host and pupal development time with spruce budworm as the host (Eq. (1)).

Parameter	In-host	Pupa
P	0.114	0.262
ρ_m	0.000	0.029
H_A	−6.149	−27.3
H_L	−34.4	−44.9
T_L	291.1	299.8
H_H	108.2	100.7
T_H	302.6	308.0
σ_ε^2	0.082	0.078

Table 2
Parameter estimates for *Tranosema rostrale*'s temperature-dependent potential fecundity (Eq. (9)) after rearing in fifth-instar spruce budworm as hosts.

Parameter	Estimate
a	−2.736
b	0.956
c	−26.971
d	2.554
κ	0.890
P_{max}	142.969

(Fig. 1; Table 1). Eq. (1), fitted to development times, very well described the responses of both life stages (R^2 = 0.99 and 0.97 for in-host and pupa, respectively; Table 1). The variation in individual development rates (σ_ε) was small for in-host (0.085) and pupal development (0.090), and was well approximated by the lognormal distribution (Fig. 1).

3.2. Stage-specific survival

The best fitting survival model had two parameters for in-host ($\beta_0 = 7.025 \pm 0.616$, $\beta_1 = -0.174 \pm 0.027$) as well as pupal development ($\beta_0 = 9.620 \pm 1.339$, $\beta_1 = -0.239 \pm 0.058$). In-host survival (Fig. 2a) was lower than pupal survival (Fig. 2b) at all temperatures, in large part because in-host survival included about 18% pseudo-parasitism (failure to lay an egg during an attack). Survival

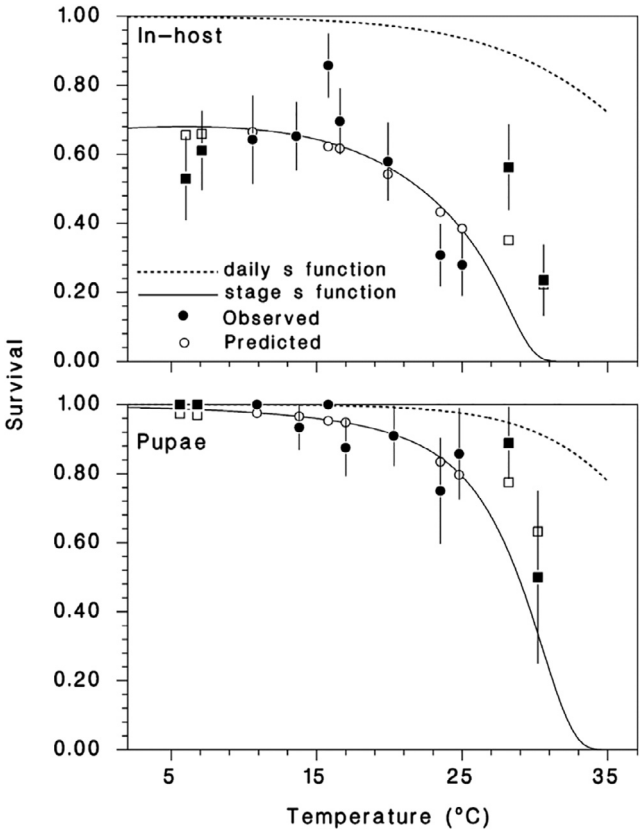

Fig. 2. Survival of immature *Tranosema rostrale* developing in spruce budworm larvae fitted to Eq. (2). Upper panel: in-host (eggs and larvae) survival (R^2 = 0.592). Lower panel: pupal survival (R^2 = 0.786). Solid line: stage-specific survival function (Eq. (4)). Closed symbols: observations (±SE of proportion), open symbols: values predicted with Eq. (2). Circles: constant temperature, squares: transfer treatments. Dotted line: daily survival function (Eq. (3)).

was highest at lower temperatures until about 20 °C, after which it rapidly decreased to near zero at temperatures >31 °C for in-host (Fig. 2a) and 34 °C for pupal development (Fig. 2b). In temperature transfers at 30 °C, only 11.8% (n = 17) of individuals completed their development to the adult stage. Survival was greatly enhanced by the use of transfer treatments at extreme temperatures of 28, 7.5 and 5 °C (50, 61 and 53%, respectively). Host mortality from causes other than parasitoid egression was about 15% between 7 and 25 °C, but about 30% at 5, 28 and 30 °C.

3.3. Adult longevity

Adult longevity decreased exponentially with increasing temperature for both male and female *T. rostrale* (Fig. 1). The parameter estimates of Eq. (5) were: $a = 5.170 \pm 0.099$, $b = 0.0707 \pm 0.0057$, and $b_m = 0.0246 \pm 0.00494$. Parameter a_m was not significantly different from zero and was dropped from the model. At all temperatures, females lived longer than males. The individual variation among our observations was unusually large ($\sigma_\varepsilon = 0.537$)) because several individuals lived much shorter lives than expected, especially at the more extreme temperatures (Fig. 1). For this reason, the variance parameter was halved for further use ($\sigma_\varepsilon = 0.268$).

3.4. Potential fecundity

The observed relationship between temperature and the mean number of eggs in the oviducts of *T. rostrale* females (potential fecundity) is described accurately by Eq. (9) (R^2 = 0.959; Table 2; Fig. 3). At 5 °C, the number of eggs increases linearly over time. With increasing temperature, the response becomes strongly non-linear. At 15 °C it reaches a plateau of about 65 eggs after 10 days. Above 20 °C, the number of eggs increases quickly in the first 3 days, reaching a maximum of about 50, 45 and 40 eggs at 20, 25 and 30 °C, respectively. After this maximum is reached at these three temperatures, the number of eggs in the oviducts decreases over time (Fig. 3). Variability in the number of eggs carried by females at any given time and temperature was high in these experiments. To generate equivalent variability among simulated females, we used the observed mean and variance of E_0 (log-normal distribution) to assign the initial number of eggs to females at emergence, and normally-distributed values of $P_{max} = 143 \pm 30$ eggs female^{-1}. The dotted lines in Fig. 3 depict the mean ± 1 SD for the expected number of eggs among simulated females.

3.5. Simulation of survival and fecundity at constant and variable temperature

Both in-host and pupal survival were predicted to be lower at variable temperatures than at constant temperatures (Fig. 4). Simulated realised fecundity was highest around 10 °C for both constant and variable temperature (about 140 eggs), decreasing rapidly to <40 eggs at 30 °C. In contrast to survival, simulated realised fecundity was always higher at variable temperature than at

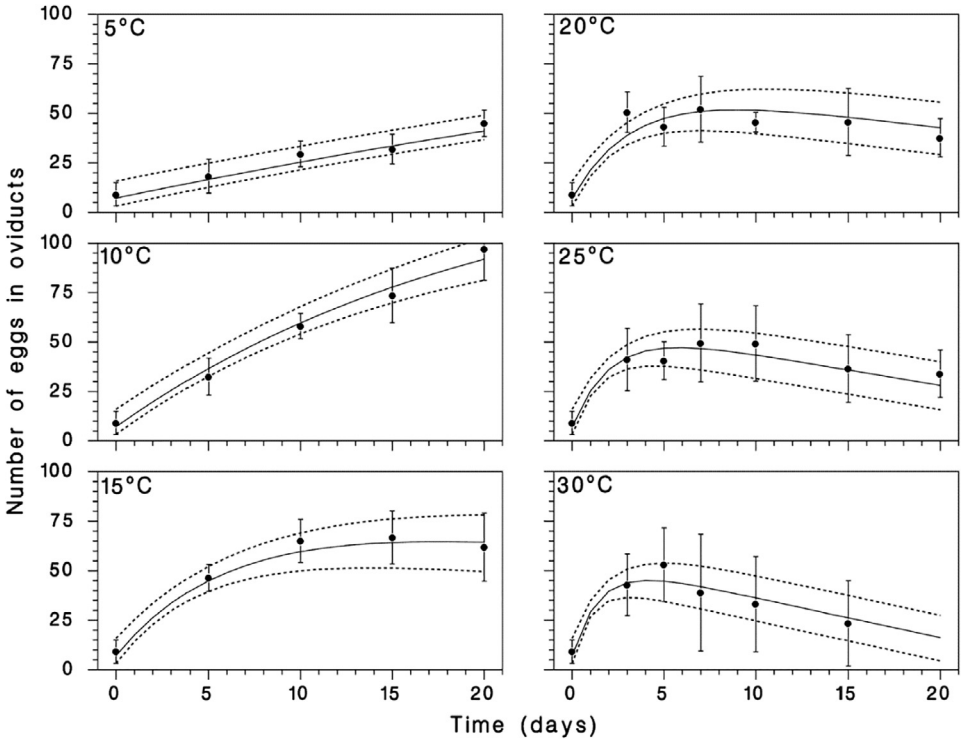

Fig. 3. Observed (circles: mean ± SD) and simulated (lines, Eq. (9)) accumulation of eggs in the oviducts of non-ovipositing *Tranosema rostrale* females at 5, 10, 15, 20, 25 and 30 °C.

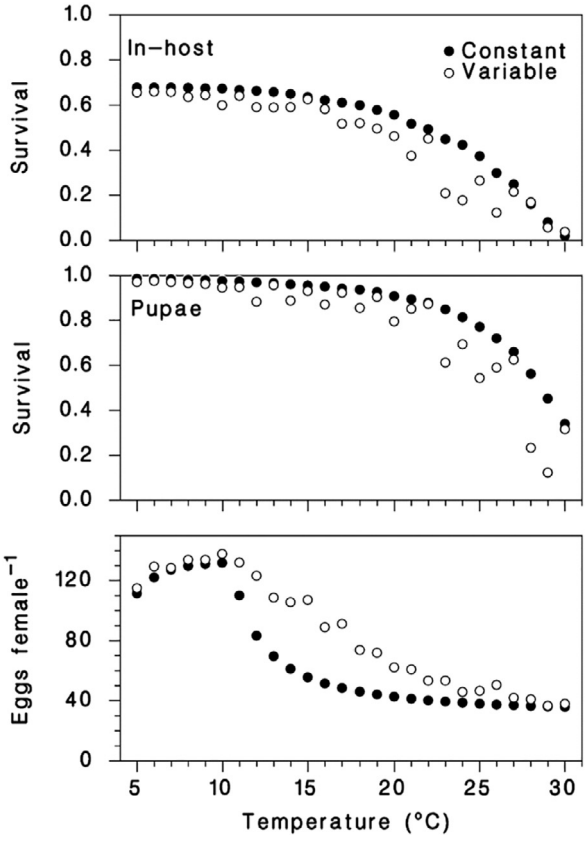

Fig. 4. Simulated probability of survival for *Tranosema rostrale* developing inside the host as an egg or larva (upper panel), and as pupae after egression from the host (middle panel), at constant (closed symbols) and variable (open symbols) temperature. Lower panel: Simulated realised fecundity of *T. rostrale* females allowed to lay all available eggs each day of their life, at constant (closed symbols) and variable (open symbols) temperature.

constant temperature (Fig. 4). In addition, the simulation of fecundity over time at variable temperature predicted that the highest oviposition rates would occur during the first few days after emergence, especially at mean temperatures ⩾10 °C (Fig. 5). While both egg production and accumulated realised fecundity were predicted to increase steadily over time at temperatures ⩽10 °C, at higher temperatures egg production decreased after the initial peak, leading to a decrease in total realised fecundity (Fig. 5). Increased longevity at a mean temperature of 5 °C and a very efficient egg production at 10 °C led to the highest predicted realised fecundity in females at these temperature regimes.

4. Discussion

Based on the laboratory and simulation results presented here, the optimal temperature for the development of *T. rostrale* was *ca.* 25 °C, while immature survival was highest below 20 °C. Adult longevity increased with decreasing temperature, and the highest realised fecundity occurred at around 10 °C. Thus, the overall fitness of *T. rostrale* appears to be maximized at temperatures below 20 °C. In the two field sites where parasitoids were collected for this study, most of the development of *T. rostrale* in its spruce budworm host takes place during June (Cusson et al., 1998; Seehausen et al., 2016a), a period when mean daily temperatures can range from 10 to 20 °C (Lethiecq and Régnière, 1988). Thus, it seems that *T. rostrale* is well adapted to the current temperature range in this region.

The impact of temperature on the survival of spruce budworm larvae has been investigated previously, and it appears to be around 95% at temperatures between 15 and 30 °C (Weber et al., 1999; Régnière et al., 2012b). Here, we found somewhat higher mortality at temperatures between 28 and 30 °C. Temperatures between 20 and 30 °C negatively affect the survival of *T. rostrale*, but not its host to the same extent. Several factors could be involved in the decreased survival of *T. rostrale* at higher

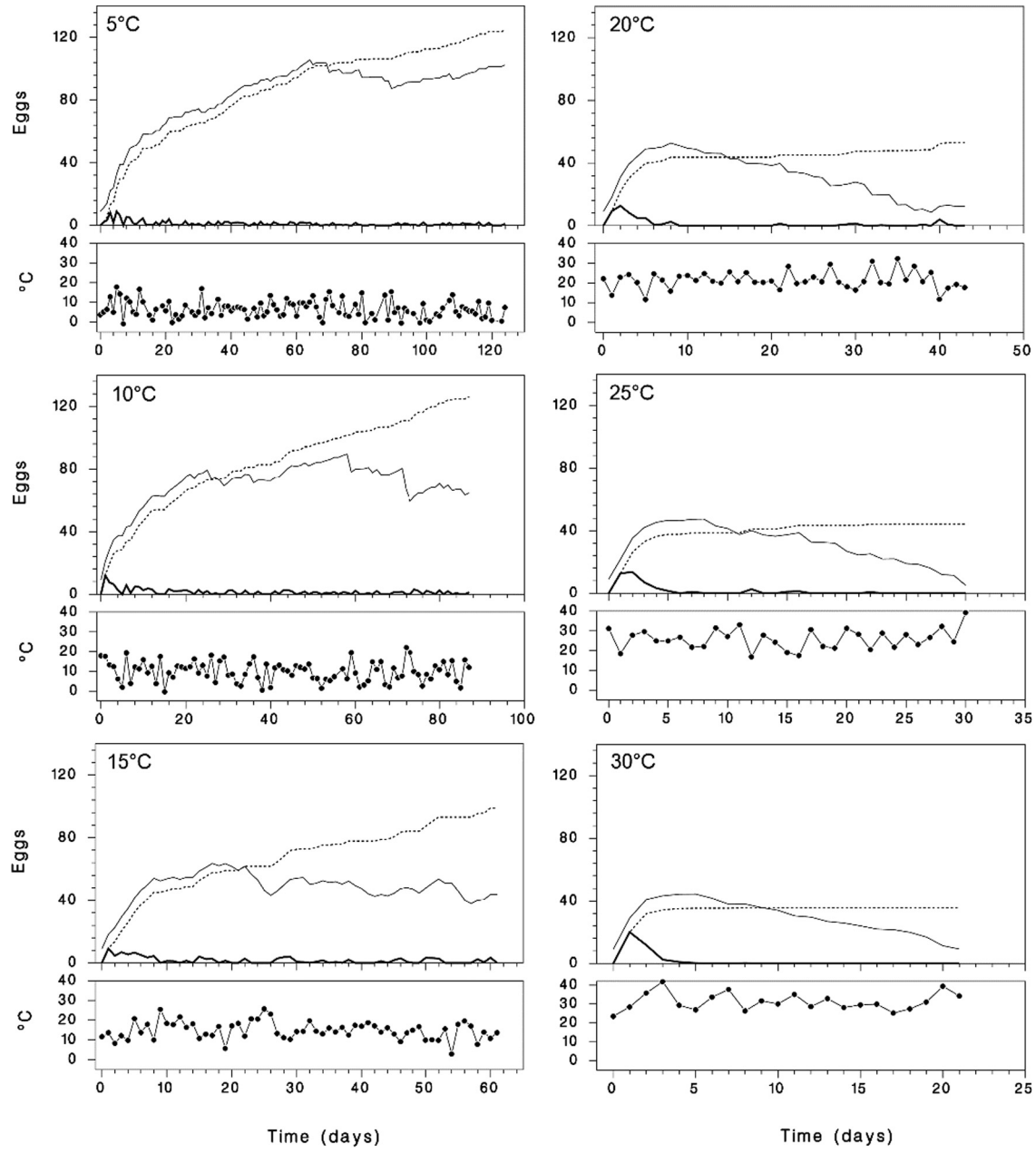

Fig. 5. Daily output of the fecundity simulation for *Tranosema rostrale* under six variable temperature regimes with means of 5, 10, 15, 20, 25 and 30 °C (σ = 5). Full gray line: egg production (*P*); dotted line: cumulative oviposition; Black line: oviposition rate; black line with black dots: daily temperature (°C).

temperatures, especially while in its host. The immune system of the host may be more efficient at high temperature (Fellowes et al., 1999; Zufelato et al., 2004), or the polydnavirus that *T. rostrale* injects into the host during oviposition (Doucet and Cusson, 1996) may be less effective at disrupting the host's immune system (Khafagi and Hegazi, 2004). Both of these explanations warrant further investigation.

Longevity of *T. rostrale* adults decreased with increasing temperature, as is commonly observed in insects (e.g. Papanikolaou et al., 2013; Andreadis et al., 2014; Cheng et al., 2015), especially in parasitoids (e.g. Spanoudis and Andreadis, 2012; Chen et al., 2015; Watt et al., 2016). Females lived longer than males at all temperatures. *Tranosema rostrale* females are generally larger than males (Seehausen et al., 2016a) and may therefore have more metabolic resources available to increase their longevity (Ellers, 1996). The larger size of female wasps may also explain the fact that females take slightly longer to develop at the pupal stage than males. Some particularly short-lived individuals were observed in our experiments, and it is possible that some of these individuals may have died from causes other than old age (e.g. handling accidents, disease or genetic conditions). These individuals were not eliminated from the analysis, and probably result in a slightly higher degree of variance in observed longevity.

The potential fecundity of *T. rostrale* at different temperatures showed a trade-off between an increasing rate of egg accumulation in the oviducts and a decreasing maximum egg load with increasing temperature. We believe this decrease in egg load is caused by increasing egg resorption at higher temperatures, a hypothesis that was formulated in Eq. (6). Egg resorption occurs in many insect taxa (Bell and Bohm, 1975) and is relatively common in hymenopteran parasitoids (Flanders, 1942, 1950; Jervis et al., 2001). In general, it is associated with anhydropic (yolk-rich) egg-producers and

species with a low ovigeny index (Jervis et al., 2001). *Tranosema rostrale* has a relatively low ovigeny index (see below), but its eggs are small (≈0.4 × 0.1 mm; Cusson et al., 1998) and appear to be hydropic. *Diadegma semiclausum*, another Campopleginae with small hydropic eggs, has also been shown to resorb eggs (Pourian et al., 2015). The simulation of realised fecundity over the lifespan of females indicates an additional trade-off between realised fecundity and adult longevity. Our results suggest that these trade-offs lead to maximum realised fecundity at 10 °C for *T. rostrale*. Under field conditions, the realised fecundity of the parasitoid is dependent on host availability.

Because our simulations of realised fecundity at variable temperature took female longevity into account, an estimated temperature-dependent ovigeny index could be calculated for *T. rostrale* by dividing the initial egg load by the potential lifetime fecundity of the parasitoid (Jervis et al., 2001). The approximate index is 0.06, 0.06, 0.09, 0.18, 0.23 and 0.3 at 5, 10, 15, 20, 25 and 30 °C, respectively. This finding underlines the importance of reporting the rearing temperature when an ovigeny index is calculated for a parasitoid or for an insect in general. The results of the fecundity simulations also suggest that *T. rostrale* has a Type-2 pattern of age-specific realised fecundity (Jervis et al., 2008): initial egg loads are relatively low and realised fecundity peaks in the first few days of the female's life; after that it declines.

To our knowledge, the fecundity model developed here is the first temperature-dependent parasitoid fecundity model to take both oogenesis and oosorption into account. The model is based on our current understanding of these two processes (Richard and Casas, 2009), and as well, takes into account the energy costs of egg resorption. It can be used to model temperature-dependent potential and predicted realised fecundity for non-host-feeding synovigenic parasitoids.

Because of the non-linearity of the temperature responses in insects, it is important that the effect of temperature variability be taken into account when estimating life history traits under field conditions. As we demonstrate here, *T. rostrale*'s survival was consistently overestimated and fecundity was underestimated at constant temperature when compared to variable temperature regimes. Physiological responses of ectotherms derived using constant temperature experiments have to be interpreted within the context of fluctuating temperatures, as it has been shown that inclusion of even daily temperature dynamics can result in important shifts in fitness profiles of insects when compared to their assessment under mean habitat temperatures (Paaijmans et al., 2013). Modeling approaches like those presented here are well suited to such interpretation, even if consequences of exposure to extreme temperatures on the recovery capacity of insects when temperatures return to normal are not taken into account.

The demonstrated detrimental impact of higher temperatures on the overall fitness of *T. rostrale* may have profound implications for the parasitoid's efficacy as a mortality factor in spruce budworm populations under conditions of changing climate. The equations and parameter estimates we have presented can be used to model the seasonal pattern of phenology of *T. rostrale* in its natural habitat to predict the seasonality of this species, which will be particularly useful in studying the interaction of *T. rostrale* with its spruce budworm host across different geographic regions and under various climatic conditions.

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