

Evolution of a physiological trade-off in a parasitoid wasp: how best to manage lipid reserves in a warming environment

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Accepted: 13 March 2013

Key words: constrained energy, ectotherms, synovigenic, dynamic programming, climate change, lifetime reproductive success, activity rate, ovigeny index

Abstract

Ectothermic animals, especially insects, are probably the ones most affected, for better or worse, by variable thermic environment, for example in the case of global warming, as their metabolic rate is controlled by the ambient temperature. Parasitoid insects, at the third trophic level, are widely distributed worldwide, and they influence the population dynamics of their highly diverse insect hosts. An important feature of parasitoid wasps is their supposedly limited or non-existent capacity to synthesize lipids during adulthood. As lipid level can be expected to determine whether they engage in maintenance or reproduction, parasitoid wasps are useful biological models for investigating how evolutionary trade-offs in energy allocation to maintenance or reproduction are likely to alter in response to global climate change. To address this, we developed a state-dependent stochastic dynamic programming model, which we parameterized using empirically derived data. The model shed light on the adaptive response of parasitoids with regard to three traits: activity rate, initial egg load, and egg production over the adult female's life span. We show that in a warmer climate, parasitoids devote smaller amounts of lipids to their reproductive effort and favour maintenance over reproduction. However, the bias towards maintenance is reduced when the parasitoids are able to adapt their activity rate to the features of their environment. This model could be tailored to a wide range of organisms with limited energy intake during their adult life.

Introduction

The effect of temperature on life history traits, metabolic rate, physiological traits, and behaviour (linked to acquisition of energetic resources and allocation of resources to different traits) is usually studied independently. However, an integrative approach is necessary to develop theories allowing to predict the adaptive responses of individuals to temperature variation (Le Lann et al., 2011). In the framework of energy budgeting in a temperature-varying environment, the evolutionary responses of individuals depend on several parameters: environmental conditions, indeed, do not only affect one or more traits in isolation but can also affect the balance of allocation of resources to

a large range of life-history traits. For example, development time is generally shorter at higher temperature, but adult body size is also lower for the majority of insects studied (Moiroux et al., 2010). The metabolic rate was also shown to evolve in relation to the amount of available resources: a higher metabolic rate, indeed, requires a higher amount of energy to maintain the body and thus fewer resources for fitness traits such as fecundity. As a consequence, a lower metabolic rate is expected when resources are limited, to reduce the rate of resource consumption (Moiroux et al., 2012). Activity is an important link between the thermal environment and an animal's life history. Therefore, activity patterns are also likely a target for natural selection (Adolph & Porter, 1993). State-dependent, stochastic dynamic programming models (Mangel & Clark, 1988; Clark & Mangel, 2000; Mangel, 2006) are a convenient tool to provide some answers to this kind of integrative question. This method permits to take into consideration the stochastic events that an

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individual can face during its lifetime, and to identify the optimal responses to these events that it can choose.

The type of responses to temperature can be assessed at two levels: (1) the effect of temperature variation on the allocation of the energy between maintenance and reproduction, and its consequence for energy allocation between immediate and future reproduction, or between egg number and egg size and (2) the effect of temperature variation on the activity rate, defined as the ability of ectotherms to exploit the environmental resources available rapidly enough, by increasing their metabolic rate. Studying evolutionary trade-offs during temperature change events, such as global climate change, can provide insights into the consequences of such change for insect populations and communities. It can, for example, inform the questions of whether the species will be more or less competitive, more or less efficient in multi-trophic interactions, and more or less subject to local extinction (Hance et al., 2007; Van Baaren et al., 2010). One feature of reproduction in insects is the timing of egg production: insects are classified according to whether they are proovigenic (all of the female's lifetime potential complement of eggs is mature when the adult emerges) or synovigenic (some or all of the eggs are immature when the adult emerges) (Jervis et al., 2001). There is in fact a continuum in the ovigeny index, which ranges from completely pro-ovigenic (ovigeny index = 1) to extremely synovigenic species (ovigeny index = 0) (Jervis & Ferns, 2011). 'Ovigeny' is a potentially unifying concept in entomology, which has been applied to several insect orders, including Lepidoptera, Hemiptera, Coleoptera, Heteroptera, and particularly to the Hymenoptera (Legaspi & Legaspi, 2008; Jervis & Ferns, 2011). It provides a relative measure of the investment in reproduction early in life that controls the total lifetime egg production, and can therefore trade-off with other life history traits (Jervis & Ferns, 2004). The fitness of terrestrial ectotherms is known to change with temperature, following a 'performance curve' (i.e., the product of the activity rate curve, metabolic level, and life span), because their performance will affect both their ability to find resources and to reproduce (Huey & Kingsolver, 1989; Addo-Bediako et al., 2000; Huey & Berrigan, 2001; Deutsch et al., 2008).

In this paper, we investigate the consequence of temperature increase on an ecologically important type of animal, a parasitoid wasp. Parasitoid wasps influence the population dynamics of a wide diversity of other insect species, including agricultural and forest pests, by driving or constraining fluctuations, and by limiting average population levels (Mills & Wajnberg, 2008). Adult female parasitoids lay their eggs in or on their host. The progeny develops and ultimately kills the host (Eggleton & Belshaw, 1992).

An important feature of parasitoid wasps is their supposedly limited or non-existent capacity to synthesize lipids during adulthood (Visser & Ellers, 2008; Visser et al., 2010). In contrast to phytophagous insects, their utilization of lipids accumulated during larval development determines the adult life span and egg production (Casas et al., 2005). In females, lipids can be allocated either to the maturation of eggs or to the adult reserves, leading to a trade-off between investment in reproduction and in life span (Ellers & van Alphen, 1997; Pexton & Mayhew, 2002). Parasitoids are known to consume energy-rich materials during foraging activities, and their metabolic rate increases with temperature (Acar et al., 2001), leading to an increase in lipid consumption (Olson et al., 2000). How parasitoids use their lipids during their adult life can therefore be expected to be influenced by temperature. Thus, parasitoid wasps are potentially valuable models for investigating the changes in trade-offs when temperature varies. To investigate these relationships, we developed a state-dependent, stochastic dynamic programming model (Clark & Mangel, 2000). We parameterized it using empirically derived data. This enabled us to examine optimum strategies regarding the initial egg load, egg-laying decisions, and oocyte maturation of synovigenic parasitoids experiencing temperature rises, comparing two scenarios of activity rate response. In the first scenario, we analyse the effect of temperature change on parasitoids that do not adapt their activity rate to the new conditions. In the second scenario, we analyse the effects of temperature on parasitoids that are able to adapt their activity rate to the new temperature. These two scenarios are both extreme. In the first case, the response of parasitoids to temperature cannot change at all, whereas in the second case parasitoid activity rate is optimally adapted to the new temperature regimes. The real scenario in the field will depend on the ability of parasitoids to adapt their activity rate to the ambient temperature, and is likely to fall somewhere in between the two situations tested, which is what we modelled and discuss below.

Materials and methods

We used a stochastic dynamic programming approach, the goal of which was to find the optimal egg load at emergence, the optimum egg-laying decisions (i.e., the number of eggs to be laid on each patch of hosts encountered), and the optimum oocyte-maturation decision (i.e., the number of new eggs to be matured each day) depending on the characteristics of the foraging habitat (Clark & Mangel, 2000). When the adults emerge, lipids accumulated during the larval stage by female parasitoids can be allocated either to reproduction or to maintenance. Let α be the

ratio of total lipids devoted to egg production at emergence. We assume that egg size is constant. To maximize their lifetime reproductive success (LRS), parasitoids should emerge with the optimal α in order to have the optimum egg load at emergence. We optimized the initial egg load and egg-laying decisions in order to determine the optimum reproductive strategies for parasitoids in environments with different characteristics (see below) and different temperatures: 15.0, 15.6, 16.2, 16.8, 17.4, and 18.0 °C.

Effect of temperature on parasitoid performance

Most studies show that an individual's maximal activity rate occurs at the mean temperature of the habitat, indicating that the activity rate has probably been shaped by natural selection (Addo-Bediako et al., 2000; Deutsch et al., 2008). To investigate the effect of temperature in our model, we used curves describing the activity and metabolic rates of parasitoids as a function of temperature (Figure 1A). We investigated two scenarios of parasitoid adaptation to temperature. In the first, we analysed the effect of temperature on synovigenic parasitoids with an activity rate adapted to the basal temperature (i.e., 15 °C). We assumed that their activity rate would not change in response to an increase in ambient temperature (no long-term effects on this activity rate). In the second scenario, we studied the effect of rising temperature on synovigenic parasitoids that are able to adapt their activity rate in response to the temperature of their environment (genetic adaptation). In this case, their basal activity rate shifted to the optimum rate for each of the temperatures tested. In both these scenarios, we assumed that the basal metabolic rate at a particular temperature does not change with temperature. We therefore assume that increasing temperature affects optimum behaviour. Parameters that change with temperature are: (1) attack rate; (2) T_h , handling time; (3) V_p , the number of lipid units used per unit of foraging time in a patch; and (4) V_T , the number of lipid units used per unit of time taken to travel between patches (Table 1). Several empirical studies have shown that both attack rate and handling time are affected by temperature (Suverkrupp et al., 2001; Flinn & Hagstrum, 2002; Menon et al., 2002; Zamani et al., 2006; Garcia-Martin et al., 2008; Gingras et al., 2008).

The attack rate and the handling time are used to describe the performance of a parasitoid as a function of body temperature (Logan et al., 1976; Huey & Kingsolver, 1989). Let $A_r(\theta)$ be the function defining the change in activity rate of a parasitoid female with temperature. Hence, if a'_0 is the value of a' at 15 °C and T_{h_0} the value of T_h at 15 °C, then, $a'(\theta) = a'_0 A_r(\theta)$ and $T_h(\theta) = T_{h_0}/A_r(\theta)$. We assume that parameters linked to activity,

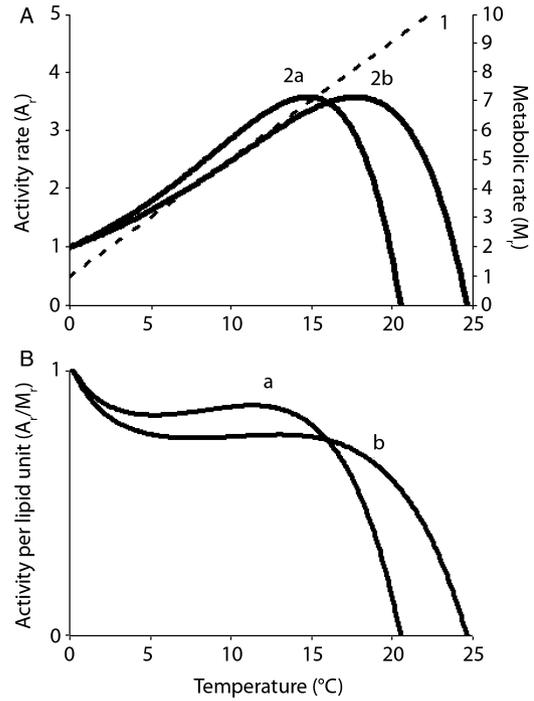


Figure 1 (A) Activity rate [A_r ; curve 1, based on equation (1) in the Material and methods section; dashed line] and metabolic rate [M_r] of parasitoids adapted to 15 °C (curve 2a) and 18 °C [curve 2b, based on equation (2); solid lines] as a function of temperature (inspired by Logan et al., 1976; Acar et al., 2001). (B) Activity per unit lipid as a function of temperature for parasitoids adapted to 15 °C (curve a) and 18 °C (curve b). The curves show the increase in activity rate, metabolic rate, and the activity per lipid unit spent. Activity rate and metabolic rate at 0 °C are both equal to 1 for parasitoids adapted to 15 °C. Parasitoids with a non-adapted metabolic rate display the activity rate and the activity per lipid unit adapted to 15 °C at each tested temperature. Parasitoids with an adapted metabolic rate display an activity rate and an activity per lipid unit adapted to each of the temperatures tested.

such as flight or foraging, also vary with temperature, following the activity rate curve of Logan et al. (1976) (Figure 1A):

$$A_r(\theta) = \psi \left[\exp(\rho\theta) - \exp\left(\rho\theta_M - \frac{\theta_M - \theta}{\Delta\theta}\right) \right], \quad (1)$$

where θ is the temperature, θ_M the maximum temperature, ψ the activity rate at 0 °C, ρ the rate of increase in activity from 0 °C to the optimum temperature, and $\Delta\theta$ the difference between the optimum temperature and a higher, lethal one. To calculate how the activity rate of parasitoids changes with temperature, values of ψ , ρ , θ_M , and

Table 1 Symbols, descriptions, and values of the main parameters used to implement the model

	Description	Units	Values
Symbol			
θ	Temperature	°C	15, 15.6, 16.2, 6.8, 17.4, 18
k	Host overdispersion parameter	–	1, 2, 3, 4, 5
m	Mean patch density	Hosts per patch	100, 200, 300, 400, 500
V_P	Amount of lipids expended in intra-patch foraging per time unit at 15 °C	Lipid units/ATU	0, 0.1, 0.2, 0.3, 0.4, 0.5
V_T	Amount of lipids expended during inter-patch travel at 15 °C	Lipid units/ATU	10
Parasitoid parameters			
a'	Attack rate at 15 °C ¹	Host/ATU	10
b	Handling time at 15 °C ¹	ATU	0.1
c_0	Lipid cost of one egg	Lipid unit	0.1
G_u	Gain of fitness per egg laid	Fitness unit	1
x	Total amount of lipids available	Lipid unit	100
Performance curve parameters			
ψ	Activity rate at the basal temperature	Activity unit	6.85
ρ	Rate of increase to the optimum temperature	Activity unit/°C	0.09
θ_M	Maximum temperature	°C	34.22
$\Delta\theta$	Width of the high temperature boundary layer in Logan's model	°C	8.33

ATU, arbitrary time unit.

¹Parameters that vary with temperature.

$\Delta\theta$ (Table 1) were determined by fitting equation 1 to experimental data on the oviposition performance of an Iranian population of the parasitoid wasp *Aphidius matricariae* Haliday (Zamani et al., 2006) at 10, 15, 20, 25, and 30 °C. Optimum performance of *A. matricariae* occurs at 25 °C. In the first scenario, we applied these data to parasitoids from temperate areas, which operate optimally at 15 °C by multiplying θ by the ratio 25/15 (Figure 1A, curve 2a). In the second scenario, the activity rate of parasitoids has evolved to fit the mean temperature in a habitat denoted by θ_H . This second activity rate is the maximum recorded for each temperature. It is calculated by multiplying θ by the ratio 25/ θ_H (Figure 1A, curve 2a and curve 2b for $\theta_H = 18$ °C).

The number of lipid units used per time unit foraging in a patch is a function of the metabolic rate of parasitoids. In ectotherms, metabolic rate increases linearly with temperature (Acar et al., 2001). Here, we assumed that lipid utilization is linked to the metabolic rate. Let $M_r(\theta)$ be the metabolic rate curve of insects as a function of temperature. We assumed that V_P , the number of lipid units expended by parasitoids per time unit foraging in a patch, would increase with temperature. If V_{P0} is the value of V_P at 15 °C, $V_P(\theta)$ should increase with temperature according to $V_P(\theta) = V_{P0} M_r(\theta)$. Acar et al. (2001) estimated the metabolic rate of an ectotherm, $M_r(\theta)$, as a function of

temperature from data on the metabolic rate of coccinellid beetles (Figure 1A):

$$M_r(\theta) = 1.036\theta + 4.29. \quad (2)$$

This expression is a linear simplification of Logan's model, considering that we work only in this almost linear part of the model (Figure 1A, dashed line). The optimum metabolic rate of the ladybeetles studied by Acar et al. (2001) occurs at 25 °C. Here, we adapted their data to our parasitoids at 15 °C by multiplying θ by the ratio 25/15.

The number of lipid units used per distance travelled between patches is a function of both the activity rate and the metabolic rate of the parasitoids. It increases both with the time spent travelling one distance unit and with the lipid cost per unit time spent travelling between patches. If V_{T0} is the V_T value at 15 °C, $V_T(\theta)$ will increase with temperature according to the Ratkowsky equation (Ratkowsky et al., 2005):

$$V_T(\theta) = \frac{V_{T0} M_r(\theta)}{A_r(\theta)}. \quad (3)$$

Both the $A_r(\theta)$ and $M_r(\theta)$ curves are plotted in Figure 1A. We used these curves to calculate the activity performed by each parasitoid per unit of lipid expended

by computing the rate of activity divided by the metabolic rate at all temperatures (Figure 1B).

We assumed that the metabolic rate did not adapt to the ambient temperature. Thus, in both the scenarios tested (parasitoids with non-adapted and adapted activity rates), lipid utilization, which is directly linked to the metabolic rate, increased from 0 to 25 °C (Figure 1A, curve 1). In this temperature interval, the activity rate increases up to an optimum temperature and then declines rapidly. Parasitoids with non-adapted activity rates presented an activity rate adapted to 15 °C at each of the temperatures tested (Figure 1A, curve 2a). Those adapted to ambient temperature always displayed the highest possible activity rate at all the temperatures they experienced (Figure 1A; activity rate adapted to 15 °C: curve 2a; activity rate adapted to 18 °C: curve 2b).

At higher temperatures, the rate of activity could offset the adverse effects of an increase in lipid expenditure. To check whether this actually happens, we calculated the amount of activity per unit of lipid spent as a function of temperature for parasitoids with an activity rate adapted to a temperature of 15 °C (Figure 1B, curve a) and for parasitoids with an activity rate adapted to 18 °C (curve b). The activity per unit of lipid is calculated by dividing the activity rate by the metabolic rate. The resulting curve shows the amount of behavioural items performed for one unit of lipid expended. Activity per unit of lipid is highest when parasitoids reach their optimum temperature, and drops when the temperature rises above this threshold. A comparison of the two figures shows that parasitoids adapted to 15 °C were more efficient at temperatures below 17 °C, whereas parasitoids adapted to 18 °C were more efficient at temperatures above 17 °C.

Activity per unit of lipid expended increases at temperatures below 5 °C. At such low temperatures, real parasitoids probably expend only small amounts of lipids, but their low level of activity is unlikely to allow them to parasitize hosts. Activity rate and metabolism curves were therefore used to implement our model and determine the optimum initial egg load, egg maturation decision, and ovigeny index of parasitoids in a warmer climate.

Habitat characteristics

As usually observed when resources are distributed in patches, the distances travelled between patches follow an exponential distribution (Hanski & Thomas, 1994; Nieminen, 1996; Hein et al., 2004). The mean and variance used to describe inter-patch distance (noted x) were $\mu = 1$ and $s^2 = 1$, respectively. Distances are thus scaled by their mean. Parasitoids use v_i lipid units per unit of distance travelled. Patch density H_p is defined as the number of hosts available in a patch. A negative

binomial distribution is commonly used to describe the spatial distribution of many species (Bliss & Fisher, 1953; Taylor, 1984; Kuno, 1991; Vos & Hemerik, 2003). For such a distribution, the probability that a patch will contain H_p hosts is denoted $P(H_p)$. A negative binomial distribution with overdispersion k and mean m is reduced to a Poisson distribution if $k \rightarrow \infty$. The relationship between the mean and variance is $\sigma^2 = m + \frac{m^2}{k}$ and $1/k$ is often known as the ‘excess of variance’. As a result, the variance between patches increases as k decreases. Finally, the cost of foraging in a patch depends on both the duration of patch foraging (t_e) and the lipid cost of patch exploitation per time unit (v_p). We assumed that patches in the habitat initially contained only unparasitized hosts, and that exploited patches were not revisited. As the hosts were being depleted over time, the parasitoids took longer and longer to find them. We measured t_{ip} the time needed to exploit a patch containing H_p hosts and to lay ω eggs using the ‘random parasite equation’ (Rogers, 1972). A parasitoid’s encounter rate with hosts is determined by the attack rate a' , and the handling time T_h :

$$t_{ip}(\omega, H_p) = -\frac{1 + a'bH_p}{a'} \ln\left(1 - \frac{\omega}{H_p}\right). \quad (4)$$

The amount of lipids expended in laying ω eggs in a patch containing H_p hosts is

$$C_{ip}(\omega, H_p) = t_{ip}(\omega, H_p)v_p. \quad (5)$$

In each scenario, we compared 150 habitat qualities using changes in the three following parameters: (1) k , the overdispersion parameter for patches; (2) m , the mean number of hosts per patch; and (3) v_p , the lipid cost of intra-patch exploitation per time unit. Five values of the host overdispersion parameter for patches were tested, $k = 1, 2, 3, 4,$ and 5 , along with five values for the mean number of hosts per patch: $m = 100, 200, 300, 400,$ and 500 . Finally, six values for the lipid costs of patch exploitation per iteration time were used: $v_p = 0, 0.1, 0.2, 0.3, 0.4,$ and 0.5 (Table 1).

The values chosen for k and m , which must be considered jointly, ensure a panel of situations ranging from very clumped ($k = 1$) to fairly random distributions ($k = 5$), and from moderate ($m = 100$) to very high densities ($m = 500$). With $k = 1$ and $m = 100$, the richness of the patches ranges from 0 to 800 or more, and the distribution curve is L-shaped, with very high probabilities of finding only 0 or 1 host. With $k = 5$ and $m = 500$, the richness of the patches range from 0 to 1 400, but the curve is bell-shaped (although right-skewed), with a low probability of

very poor patches. Low densities were discarded, because they were very difficult to manage in the simulations and led to very low fitness with large variances. As an example, in a run of 1 000 patches with $k = 1$ and $m = 10$, almost 50% of the patches contain fewer than five hosts. In this range of values, the difference in fitness obtained at the end of life is noticeable and clearly responds to temperature, which is the main topic of this study.

It was more difficult to choose the range for the values chosen for the cost of patch exploitation, as no data are available in the literature. We chose a small value, compared both to the cost of travelling between patches and to the lifetime reserves of the animal, including the extreme and unrealistic value of zero. Among non-zero values, we used a range of 1–5 as a reasonable hypothesis for the variability of this parameter. Of course, as in any simulation model, our conclusions will be restricted to the range of parameters explored.

Optimum initial egg allocation and egg-laying decision strategies

Our model is inspired by that of Ellers et al. (2000). Through dynamic programming, we optimized the LRS function by means of backward iteration, starting at the maximum age (t_{\max}) and assuming that each individual acts optimally at every time step (Clark & Mangel, 2000). Adult parasitoids emerge with a finite number of eggs and a reserve of lipids accumulated during the larval instar that they subsequently use to survive, l (here, $l = 100$ lipid units). At emergence, a fraction $\alpha_l = l_a$ goes to activity and the complement $(1 - \alpha)l = l_b$ goes to eggs. The lipid cost of producing one egg before or after emergence, c_{egg} , is equal to 0.1 lipid unit. Thus, at emergence, the lipid reserve, designated R , is equal to l_a , and the egg load, designated E , is equal to $10l_b$.

The expected reproductive success in the next patch of a parasitoid with lipid reserves R and egg load Ω depends on the probability that it will find a patch (P_p) and the number of eggs it will lay in it. The probability of reaching a patch is given by the proportion of the distribution of the lipid cost of travel, $t_c = v_T(\theta)x$, where x is the inter-patch distance, that is lower than the lipid reserves R . If the lipid cost of searching for a host patch exceeds the parasitoid's lipid reserves, the parasitoid does not reach. The predicted cost of travelling $C_t T_p$ for a parasitoid finding a patch is then estimated as follows:

$$C_t = \sum_{i=0}^R P(c_t = i|\theta)^i. \quad (6)$$

Parasitoids can decide to exploit the patch encountered partially, f corresponding to the percentage of hosts attacked by the parasitoid in a patch. In a patch containing

H_p hosts, the maximum number of eggs a parasitoid can lay is limited by its egg load Ω and its expected lipid reserve R . After each inter-patch journey, the lipid reserve remaining is $R - T_p$. Let ω_{\max} be the maximum number of eggs that the parasitoid can lay in a patch of H hosts after each inter-patch journey. ω_{\max} is thus the maximum value of ω for which the condition $C_{ip}(e|H_p) < R - T_p$ is preserved. The number of eggs ω_l laid by parasitoids with a lipid reserve, R and egg load, Ω in a patch containing H_p hosts is then:

$$\omega_f = \min(fH_p, \Omega, \omega_{\max}). \quad (7)$$

The expected number of eggs (Ω_p) laid in a given patch is limited by the number of hosts available H_p , by the egg load Ω , or by the egg-laying decision of the parasitoid:

$$\Omega_p = \sum_{j=0}^{H_{p\max}} P(H_p = j|\theta, k, m)\Omega_f, \quad (8)$$

where Ω_f stands for the expectation of ω_f .

The expected cost of intra-patch foraging (C_{ip}) is given by:

$$C_{ip} = \sum_{l=0}^{H_{p\max}} P(H_p = l|\theta, k, m)M_p(\omega_f|H_p), \quad (9)$$

where M_p is the amount of lipid the parasitoid decides to allocate to egg maturation after visiting patch p . M_p is thus limited by the lipid reserve after visiting the patch p : $R - T_p - C_{ip}$. Each unit of lipid allocated results in $\frac{1}{c_o}$ eggs, the expected number of eggs that mature (E_m) after visiting a patch is thus equal to $M_p c_o$. The number of eggs to be laid in a patch is determined by maximizing the fitness function $F(R, \Omega, p)$, for a parasitoid with energy reserves R , having Ω mature eggs at step p . The dynamic programming equation for a parasitoid's LRS is thus:

$$F(R, \Omega, p) = P_p \left\{ \Omega_p + \max_{f, M_p} [F(R - T_p - C_{ip} - M_p, \Omega - \Omega_p + \Omega_m, p+1)] \right\}. \quad (10)$$

The rank of the patch, p , stands here for the time. It means that the unit of time is the time necessary to travel between two patches and to exploit the last. All is conditioned by the fact that the animal actually finds a new patch (P_p). In the patch $p + 1$, the reserves R available at step p are depleted by the energy spent in inter-patch travel (T_p), by that spent in intra-patch foraging C_{ip} calculated as defined in equation (4), and by the amount of energetic reserves that it decides to allocate to egg maturation (M_p)

which is one of the two variables subject to optimization. The egg load available at step p is increased by the number Ω_m (7) and decremented by the number of eggs laid. Equation (10), following the SDP equations proposed by Mangel (2006), describes the expected fitness of a parasitoid with energy reserves R and egg load Ω before it visits patch p . The expected fitness is calculated for each possible number of egg-laying decisions ($f = 0, 1, \dots, 100$) and for each possible decision of lipid allocation to egg maturation ($M_p = 0, 1, \dots, T_p - C_p$). The optimum allocation at emergence is defined as the initial egg load associated with the highest expected LRS. As usual, the calculation begins at the end of life, in the last patch visited and is iterated backward. The optimal solutions for f and M_p are recorded at each step.

Egg load and egg-laying decisions during life

Solving equation 10 by means of backward iteration gives the optimal initial allocation at the different tested temperatures, as well as the predicted egg-laying decisions as a function of the lipid reserves and egg load of the parasitoid. For each habitat and each temperature, we then used a forward iteration to model the effects of each habitat's characteristics on egg-laying decisions made by 5 000 wasps adopting the optimum initial allocation (Mangel & Clark, 1988; Clark & Mangel, 2000). To do this, the profitability of each patch encountered is randomly generated from a binomial negative distribution, and the distance of all inter-patch travel is randomly generated from an exponential distribution, as described above. The LRS, the optimal initial egg load, the number of eggs laid per patch, and the proportion of lipid reserves used for patch exploitation were recorded for every patch visit, and for all simulated parasitoids. Egg load and egg maturation decisions were used to estimate the ovigeny index. Simulations were performed for 5 000 parasitoid females and 150 habitats at the six temperatures tested, leading to a total of 4 500 000 runs. All simulations were performed with MATLAB R2008b software (Mathworks, Natick, MA, USA).

Statistical analysis

All dependent variables were analysed by means of multiple regression, testing for the effect of the following four continuous predictors: (1) host overdispersion parameter (k); (2) intra-patch foraging costs (V_p); (3) mean patch density (m); and (4) ambient temperature (θ). We evaluated the effects of continuous predictor variables on all recorded dependent variables. Statistical analyses were performed using STATISTICA 6 software (Statsoft France 2003, Maisons-Alfort, Val-de-Marne, France).

Results

Parasitoid foraging behaviour and lifetime reproductive success

Habitat quality is determined by the host clumping parameter k , the mean patch density m , which determines the probability of finding high density patches, and the lipid cost of intra-patch exploitation per unit time v_p . The effect of each of these parameters is detailed in Table S1. Regardless of habitat quality parameters, temperature (θ) affects the foraging behaviour, and thus the LRS of parasitoids (Figure 2). In response to an increase in temperature, the parasitoids made fewer inter-patch trips (θ ; Tables S1 and S2E) and parasitized fewer hosts within patches (θ ; Tables S1 and S2F). Furthermore, both the foraging behaviour and the LRS of individuals with adapted activity rates were less affected by the increase in temperature than those of individuals unable to adapt their activity rate in response to changes in the environment.

Initial egg load, egg maturation decision, and ovigeny index

Parasitoids with non-adapted activity rate showed us how parasitoids are likely to behave in response to an increase in temperature, despite a lack of adaptation to higher temperatures. In this case, the LRS of a parasitoid depends solely on its lipid management. Both the initial egg load and egg maturation during adult life decreased with temperature (Figure 3, and Tables S1, S2B, and S2C). An increase in temperature caused a decrease in the rate of activity per lipid unit, which in turn increased the cost of foraging. By decreasing their total egg load (15% fewer eggs produced at 18 °C compared to 15 °C), parasitoids devoted more of the lipids available to maintenance and foraging, and therefore were able to bear the supplementary costs of foraging due to the temperature increase. Synovigenic parasitoids can reduce the total number of eggs they produce during their life by reducing their initial egg load and/or by allowing fewer eggs to mature during their adult life. Our results indicate that the parasitoids are more likely to favour the second solution: they reduce egg production during adult life and not at emergence. As a result, the ovigeny index increases from 0.792 at 15 °C to 0.824 at 18 °C. Due to their shorter life expectancy, parasitoids can be expected to emerge with more mature eggs, because of the increased probability that they will die before they can mature any further eggs.

Parasitoids with an adapted activity rate displayed less impact of temperature on their foraging behaviour. As a result, at high temperatures, parasitoids with an adapted activity rate allocated fewer lipids to maintenance and foraging than parasitoids with a non-adapted activity rate. The parasitoids with an adapted activity rate reduced their total egg load by only 6% at 18 °C, compared to 15% for

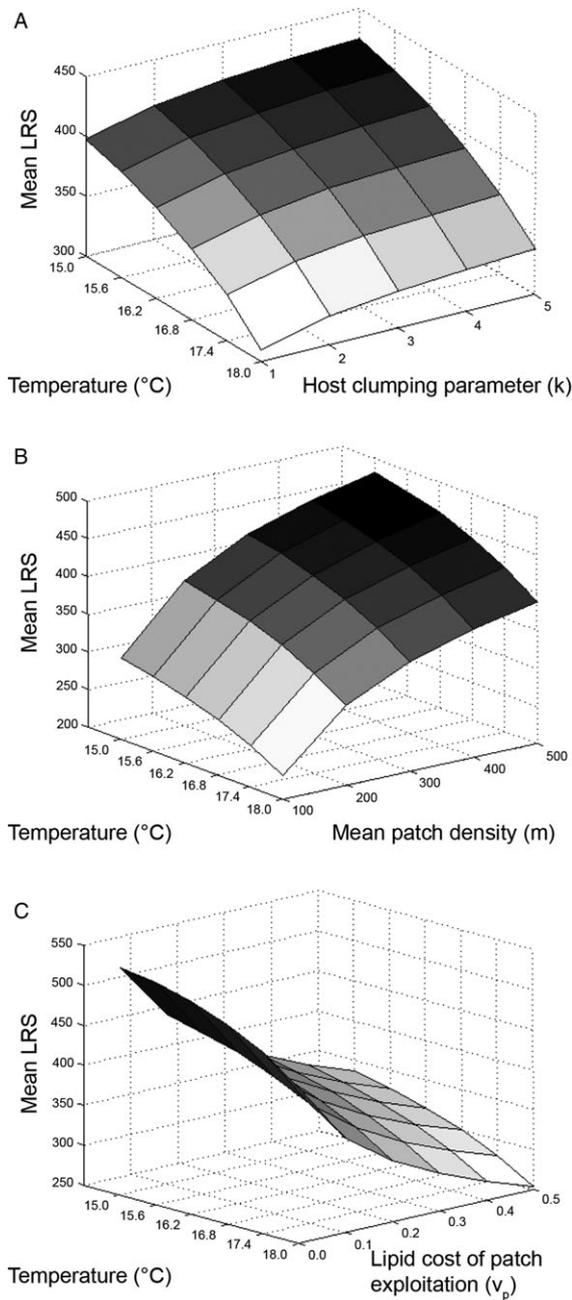


Figure 2 Mean lifetime reproductive success (LRS) of parasitoids with a non-adapted activity rate as a function of temperature and (A) host clumping parameter, k , (B) mean patch density, m , and (C) intra-patch foraging cost per unit time, v_p .

parasitoids with non-adapted activity rate. Moreover, at 18 °C, the ovigeny index of parasitoids with an adapted activity rate did not change significantly (Figure 3 and Tables S1 and S2D). Due to their activity rate adaptation, the life span of parasitoids was not much shorter, and the

optimum balance between the initial egg load and the number of eggs matured during adult life was close to what it was at 15 °C. In conclusion, in response to an increase in temperature, parasitoids allocate more lipids to maintenance and foraging to the detriment of the total number of eggs they allow to mature during their life span. However, the better the parasitoids perform (i.e., the higher their activity rate) in response to climate change, the less adaptation is made of the initial egg load or the number of eggs matured during adult life.

Discussion

Fitness decreases under warmer conditions

Our results show that at increased temperatures, for example resulting from climate change, the LRS of most species is lower, regardless of the habitat they exploit. Many studies have predicted that parasitoids, and more generally insects at the highest trophic levels, will suffer in a warmer climate (review in Hance et al., 2007). Many of the effects of temperature increase are confounded and, of course, very difficult to disentangle (Hance et al., 2007). This is why we worked on the ‘performance curve’, which is the most complete representation available of the cumulative effects of different variables on fitness, and with a modelling approach, which has the advantage that, in a simulation grid, the different variables and effects can be orthogonalized, as we did here by using a factorial design.

Our results support the idea that, when temperature increases, lipid limitation will affect parasitoids by constraining their ability to exploit the habitat. In non-adapted parasitoids, the loss of LRS reaches 21 vs. 8.6% for adapted parasitoids (Table S1). As Darwinian adaptation requires the additive effects of genetic variance over many generations for the traits to respond to temperature, we can predict that there would be a transition period with a major loss of fitness if climate change is sudden, and that it would take a long time to reach a new adaptive state. Furthermore, this new state will be less efficient than the initial one. By extension, most ectotherm species are subject to energy constraints, and so their foraging activity would also decrease.

Reproduction at higher temperature: allocation of energy to maintenance and reproduction

In a previous study evaluating the short-term consequences of climate change, we showed that in warmer climates parasitoids are likely to adopt longer patch residence times (Denis et al., 2011). Here we show that parasitoid wasps are also likely to respond by decreasing their fecundity both by lowering their initial egg load and by maturing fewer eggs during adult life and thus favour

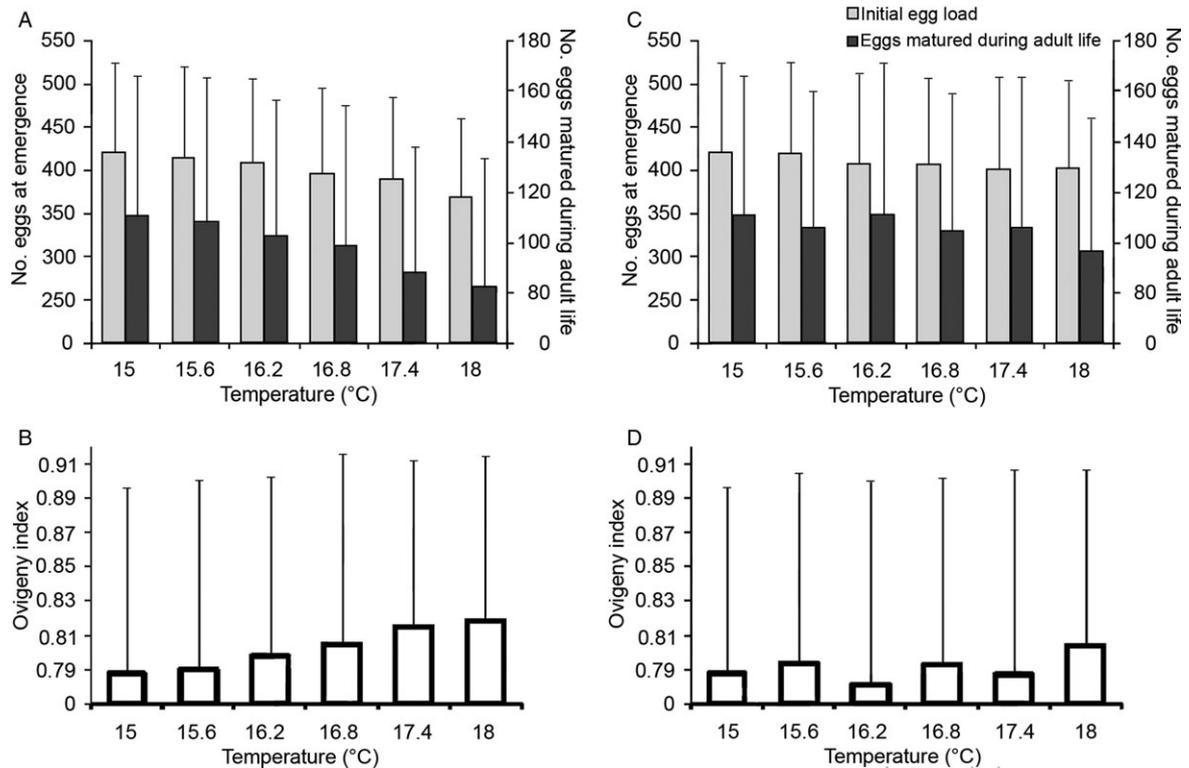


Figure 3 Mean (+ SD) (A,C) number of eggs at emergence and eggs matured during adult life of parasitoids and (B,D) ovigyny index of parasitoids, with (A,B) a non-adapted activity rate and (C,D) an adapted activity rate response, as a function of temperature. Sample size = 5 000 for the 150 habitats tested in each case.

maintenance over reproduction. Our results also indicated that the adaptive response of parasitoid performance (i.e., an increase in the activity rate) at higher temperatures will in fact attenuate the impact of temperature increase on the trade-off between reproduction and maintenance. By extension, this effect can also be predicted for all ectotherm species which have limited energy available. Indeed, all organisms face the problem of when to allocate more resources to reproduction than to other life-history processes, such as growth, dispersal, or maintenance (Thorne et al., 2006). Theoretical modelling (McNamara & Houston, 1996; Clark & Mangel, 2000) suggested that allocation of resources to different functions is not fixed but varies as resources vary, which in turn is strongly dependent on abiotic factors, such as climatic conditions.

A warmer climate can also be expected to lead to a modification in the ovigyny index of ectothermic insects. Our modelling shows that the relative decrease in initial egg load compared to the decrease in the number of eggs matured during adult life favours a higher ovigyny index. However, even though the ovigyny index of non-adapted parasitoids increased significantly with tempera-

ture, no significant ovigyny index change with temperature was observed in adapted parasitoids. This was probably due to the compensation between the two adaptive mechanisms, i.e., between the adaptation of the activity rate and the change in the reproduction-maintenance trade off.

Predictions and field studies

Field studies have already provided evidence of intra-species variations in the ovigyny index. For example, in the cabbage white butterfly, *Pieris napi* L., Larsdotter Mellström et al. (2010) showed that the ovigyny index depends on the season: diapausing females have more mature eggs at emergence than non-diapausing ones, and they also displayed differences in associated life-history traits. This highlights the importance of climatic conditions in shaping life-history traits. Moiroux et al. (2010) recently compared the life-history traits of five populations of *Leptopilina boulardi* Barbotin et al., a *Drosophila* parasitoid originating from areas with contrasting climates. They found that populations from warmer areas tended towards pro-ovigyny and that the habitat characteristics

explain the ovigeny index pattern better than temperature in these populations. Their results confirmed that parasitoids respond to habitat modification by adapting their ovigeny index, inducing inter-population variations in the ovigeny index. Our simulations led to similar predictions. By increasing the relative costs of foraging, higher mean temperatures can be expected to select for pro-ovigenic (high ovigeny index-related) traits. Nevertheless our results, like those of other studies (Ellers et al., 2000), confirm that, for moderate differences of temperature, habitat characteristics can explain the observed ovigeny index better than climatic characteristics.

Biological control: impact of parasitoids on host insect populations in a warmer climate

Parasitoids play a significant role in the population dynamics of numerous host insect species. Our results showed that in a warmer climate, the host–parasitoid relationship will be affected in two ways. First, at higher temperatures, the mean proportion of hosts attacked per patch will not noticeably decrease, but parasitoids will reduce the number of inter-patch journeys. Thus, parasitoids show a similar efficiency in their foraging behaviour, but visit fewer patches during their lives. Second, fitness changes with temperature, following the performance curve described by Huey & Kingsolver (1989), Addo-Bediako et al. (2000), Huey & Berrigan (2001), and Deutsch et al. (2008). As the performance curve drops when temperature deviates from the optimum value, the fitness of the host species can also be expected to drop at higher temperatures. Hosts can benefit from their ability to synthesize lipids in contrast to parasitoids (Visser & Ellers, 2008; Visser et al., 2010). The outcome will depend on whether the hosts or parasitoids are more affected by the temperature increase.

Acknowledgements

This work was supported by the ANR CLIMEVOL. We are grateful to Valérie Briand for technical help. We thank Drs. Jacintha Ellers, Frederic Hamelin, and Jacques van Alphen for their comments on the model. We are also particularly grateful to Dr. Mark Jervis for his detailed reading of the manuscript. We thank Monica Ghosh for improving our English. We also thank Dr. Mark Mangel and another, anonymous referee for their critical reading of a previous version that helped us to improve the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Mean treatment effect of the model parameters on lifetime reproductive success (LRS), optimum initial egg load, oocyte maturation, optimal ovigeny index, inter-patch travel, and proportion of hosts attacked per patch of parasitoids with a non-adapted or an adapted activity rate.

Table S2. Multiple regressions of mean (A) lifetime reproductive success (LRS), (B) optimal initial egg load, (C) oocyte maturation, (D) optimum ovigeny index, (E) inter-patch journeys, and (F) proportion of hosts attacked per patch by parasitoids with a non-adapted or an adapted

activity rate. The β coefficients, obtained from standardized variables ($X = 0$ and $SD = 1$), show the relative contribution of each independent variable in predicting the dependent variable.