Role of ageing and temperature in shaping reaction norms and fecundity functions in insects

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Abstract

The existing energy partitioning models assume that fecundity is constant throughout adult life. In insects, however, fecundity is a triangular function of time: after maturation, it initially sharply increases and after reaching its maximum it slowly declines as the mother ages. These models also fail to explain that empirical data generally indicate an increase in juvenile growth rate caused by improvement in food quality results in larger adults, whereas that caused by an increase in ambient temperature results in smaller adults. This 'life history puzzle' has worried many biologists for a long time.

An energy-partitioning model for insects is presented with soma and gonads as its components, which – contrary to other models – assumes ageing of soma. This model explains the triangular shape of the fecundity function, and also offers an explanation of the 'life history puzzle'. The differential response in adult size to changes in food quality and temperature in nature may result from the differential responses of our model's parameters to changes in these environmental parameters. Better food quality results in bigger adults, because food quality affects the assimilation rate, but not the rate of conversion of gonadal biomass into offspring, or the rate of senescence. In contrast, an increase in temperature speeds up all the processes. That is, temperature affects the assimilation rate, the conversion rate of gonadal biomass into offspring, and the rate of senescence equally. Therefore, an increase in temperature results in larger or smaller adults, depending on the shape of the senescence function.

Introduction

Energy partitioning models are often used to explain phenotypic plasticity, particularly the trade-off between age at maturity and adult size (e.g. Ziolko & Kozlowski, 1983; Kozlowski & Wiegert, 1986; Sibly & Calow, 1986; Kozlowski, 1992; Stearns, 1992), and more recently also to explain differential responses to changes in temperature and food quality (Berrigan & Charnov, 1994;

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Sevenster, 1995). Fecundity is assumed to be (usually linearly) dependent on adult size, which is assumed to remain constant throughout adulthood (Ziolko & Kozlowski, 1983; Kozlowski & Wiegert, 1986; Stearns, 1992; and partially Sibly & Calow, 1986). This means that fecundity is also constant throughout adult life. This may be true for some organisms, but is not true for most insects, the largest group to which these models can be applied. The typical iteroparous insect fecundity function is triangular: a steep increase of fecundity immediately after the onset of reproduction is followed by a slow decline, as the organism ages (Roff, 1992). We are not aware of any model that takes this into account, or any rigorous explanation of why the fecundity function has this shape.

The von Bertalanffy curve is often used to describe immature growth (e.g. Stearns, 1992; Berrigan &

Charnov, 1994; Berrigan & Koella, 1994; Sevenster, 1995). However, the typical insect larval growth curve is exponential or sigmoidal (e.g. Brough *et al.*, 1990; Roff, 1992), i.e. at least initially curved up, not down like the von Bertalanffy curve.

In the majority of energy partitioning models, many conclusions emanate from the assumption of a negative trade-off between mortality rate and growth rate (e.g. Stearns, 1992) or the proportion of energy devoted to growth (e.g. Sibly & Calow, 1986). A higher growth rate can entail a mortality cost, especially when activity levels or habitat choices that result in faster growth expose the organism to a greater risk of predation. It is not clear, how crucial this assumption is for the evolution of insect reproductive strategies.

Mortality is usually incorporated into models by means of a constant mortality rate in the Euler–Lotka equation (e.g. Sibly & Calow, 1986; Stearns, 1992), or by means of a fixed life span (e.g. Ziolko & Kozlowski, 1983). However, those studies have not considered the effect of ageing.

This paper considers the effect of ageing on energy partitioning, in particular its role in shaping the fecundity function, juvenile growth curve, reaction norm, and response in adult size to changes in temperature and food quality.

The model

We assume that an insect's body consists of two basic parts, both of which are functions of time, t: soma, $s = s(t)$ and gonads, $g = g(t)$ (see Table 1 for notation). The initial (birth) sizes of these components are $s(0) = s_0$ and $g(0) = g_0$, respectively. The net energy production, P, is an allometric function of the somatic size, $P = nas^\alpha$, where $0 < \alpha < 1$ and is distributed to support further growth of soma or is devoted to increase of gonadal size according to a control function $u(t)$, $0 \le u(t) \le 1$ for any positive t: the amount $u(t) \times P$ is devoted to further increase of soma and the amount $[1 - u(t)] \times P$ is devoted to further increase of gonads. In contrast to the increase of soma or gonads, energy cannot be used for immediate offspring production, for which a certain time is necessary. The energy has to be first converted into offspring and this involves very complicated processes at the cellular level that are rate limited (Maynard Smith, 1969). Mathematically, this conversion means there is a maximum rate, M, at which a unit size of gonads can produce offspring. Fecundity, F, is therefore a product of gonadal size and the control function $v(t)$, $0 \le v(t) \le M$ for any positive t: $F = v(t)g(t) \le Mg(t)$. The negative effect of senescence, $n = n(t)$, is a continuously differentiable function, equal to one at the instant of maturity (no senescence), decreasing with age ($n' < 0$, where ′ denotes the first derivative), and approaching zero as age increases. This function causes the net production, P, available for growth and/or reproduction to approach zero in old

Table 1 Notation.

Value	Description
t	Time
$s = s(t)$	Somatic size at time t
$g = g(t)$	Gonadal size at time t
s_0	Somatic size at birth
g_0	Gonadal size at birth
a	Assimilation rate
α	Scaling constant (slope of the relation between somatic size and its energy production on a log–log scale)
λ	Mortality rate
M	Maximum rate of conversion of gonadal biomass into offspring
$n = n(t)$	Senescence function
d	Rate of senescence
$P = P(t)$	Somatic production
r	Fitness measured as population growth rate
D	Age at maturity
t_0	Age after maturity at the peak reproduction
$u = u(t), v = v(t)$	Control functions

age ($P = nas^\alpha \ge 0$ for any t, but $\lim_{t \to \infty} P = 0$). Mortality rate, λ, is a constant, as in most similar models. This leads to the following system of equations:

$$s' = nas^\alpha u \qquad s(0) = s_0 \qquad (1a)$$
$$g' = nas^\alpha(1 - u) - vg \quad g(0) = g_0 \quad (1b)$$

The value to be maximized is fitness, and following the usual practice (Sibly & Calow, 1986) this is assumed to be equivalent to the value r in the Euler–Lotka equation:

$$\int_0^\infty vg\, e^{-(r+\lambda)t}\, dt = 1. \qquad (2)$$

An appropriate choice of units for mass enables us to set $s(0) = 1$. It is also reasonable to assume $g(0) = 0$, as most insects either do not have any gonads at birth, or the gonadal birth size is minute and can be ignored. Senescence has a minimal effect, if any, during the immature stage and can be ignored when juveniles are considered. Because of the linearity of the control functions u and v, the optimal solution is 'bang-bang': with $u(t) = 1$ initially, for $t \le D$, followed by a switch to $u(t) = 0$ afterwards (Cesari, 1983). The v function can be of any form for $t \le D$, and $v(t) = M$ for $t > D$. All this simplifies the model, which then becomes

$$s' = as^\alpha \quad s(0) = 1 \quad \text{for } t \le D \qquad (3a)$$
$$g' = 0 \quad g(0) = 0 \qquad (3b)$$
$$s' = 0 \qquad (3c)$$
$$g' = nas^\alpha - Mg \quad g(D) = 0 \quad \text{for } t > D, \qquad (3d)$$

with the constraint

$$\int_D^\infty Mg\, e^{-(r+\lambda)t}\, dt = 1, \qquad (4)$$

in which r is maximized with respect to D. The instant of ▮1 the switch from pure growth to pure reproduction, D, can be obtained numerically for various values of parameters a (assimilation rate), M (maximum conversion rate) and of the function n (effect of senescence). The constant α is commonly assumed to be about 0.75, which is used in the simulations published here, but the results are not sensitive to changes in this value. In our simulations the function $n(t) = \exp(-dt^2)$ was used and an appropriate choice of units for time enabled us to set $d = 0.1$, which greatly reduces the number of simulations necessary to test the robustness of the predictions.

Results

The fecundity function produced by the model very closely resembles that observed in insects. Its shape is determined by senescence, i.e. the term n in the second equation of the model. As n is continuously differentiable, g is also continuously differentiable for any t. As $n(D) = 1$, and n is continuous, it is $P(t) > 0$ and therefore $g' > 0$ in some interval $<D; D + t_0>$, where t_0 is positive. As $n' < 0$, it is $P' < 0$ for any t. If $g' = 0$, then $g'' = P' < 0$ and thus g reaches its maximum in this instant. Therefore, because g is continuously differentiable, it has only one extreme – a maximum – and declines afterwards. As $\lim_{t \to \infty} P = 0$, it is also that $\lim_{t \to \infty} g = 0$. In summary, $g(0) = 0$, g increases in some interval $<D; D + t_0>$, declines in $<D + t_0; +\infty>$ and approaches zero as $t \to \infty$. Fecundity, Mg, follows exactly the same pattern. Some examples of this fecundity function are given in Fig. 1. Setting $d = 0.1$ results in the duration of the reproductive life being about 20–40 units, which corresponds to reality in insects, when time is measured in days.

From the first equation in (3) it follows $s'' = \alpha \, a s^{\alpha - 1} > 0$. Thus the juvenile growth curve predicted by the model is always curved up, which is exponential growth. For a broad range of parameter values the model predicts that the ratio of developmental time to life span is about one half (Fig. 2). T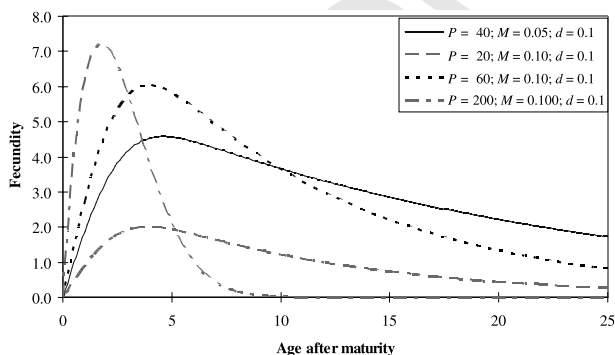he ratio of population to individual growth rate, r_m/RGR, is always smaller than one, strongly increasing with increase in a and weakly so with increase in M (Fig. 3).

It is evident from (3) that adult size increases with increase of the values of the parameter a, for constant M and d; one example is shown in Fig. 4a. When all three parameters, a, M, and d increase at the same rate, adult size predicted by the model increases or decreases depending on the shape of the senescence function, n (see Appendix for proof). Results of one simulation leading to decrease in adult size are shown in Fig. 4b.

Discussion

Inclusion of the senescence function and of the maximum conversion rate, M resulted in a triangular shaped fecundity function. If the latter were omitted, the result of the optimization procedure would be: convert all gonadal biomass into offspring immediately after maturation and subsequently all incoming energy into offspring resulting in gonads of size zero during the whole adult life.

The curved up shape of the juvenile growth curve predicted by the model is consistent with many empirical observations (Brough *et al.*, 1990; Roff, 1992).

Wyatt & White (1977) use an empirically derived equation to estimate the population growth rate for aphids and mites, in which they implicitly assume that the reproductive period is equivalent to the developmental period. Our results (Fig. 2) lend some theoretical support for this empirically derived equation.

In an earlier work it was shown that the upper limit for the ratio of population to individual growth rate is in the region of 0.86 (Kindlmann *et al.*, 1992). Results shown in Fig. 3 suggest that this ratio can only be achieved, if both a and M are large, i.e. if the organism is especially effective at converting food into growth and offspring.
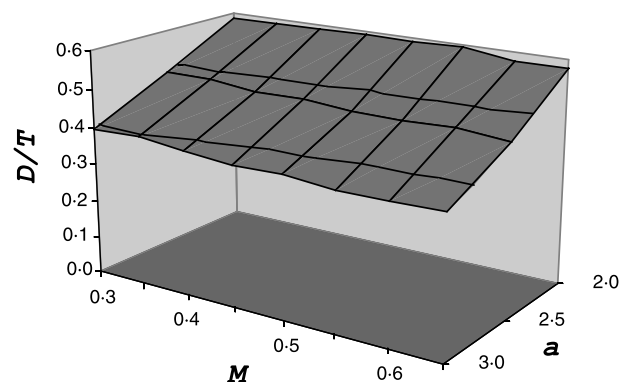

Fig. 1 Fecundity as a function of age after maturity predicted by model (3). Parameters indicated in the inset.

Fig. 2 The ratio of age at maturity, D, to the life span, T, plotted against the maximum conversion rate of energy into offspring, M, and against assimilation rate, a, predicted by model (3). Parameter $d = 0.1$.
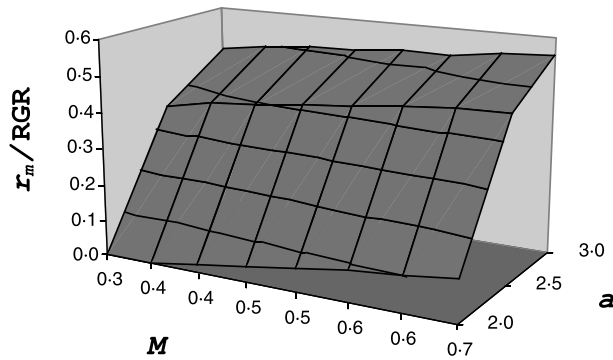
Fig. 3 The ratio of population growth rate, r_m, to the growth rate of an individual, RGR, plotted against the maximum conversion rate of energy into offspring, M, and against assimilation rate, a. Parameter $d = 0.1$.

Many empirical data indicate that an increase in juvenile growth rate caused by improvement in food quality results in larger adults, while an increase in juvenile growth rate caused by increase in ambient temperature results in smaller adults. This 'life history puzzle' (Sevenster, 1995) has worried many biologists for a long time. van der Have & de Jong (1996) predict temperature-dependent size variation of ectotherms at maturation as a result of the interaction of growth and differentiation. Their model aims to clarify how temperat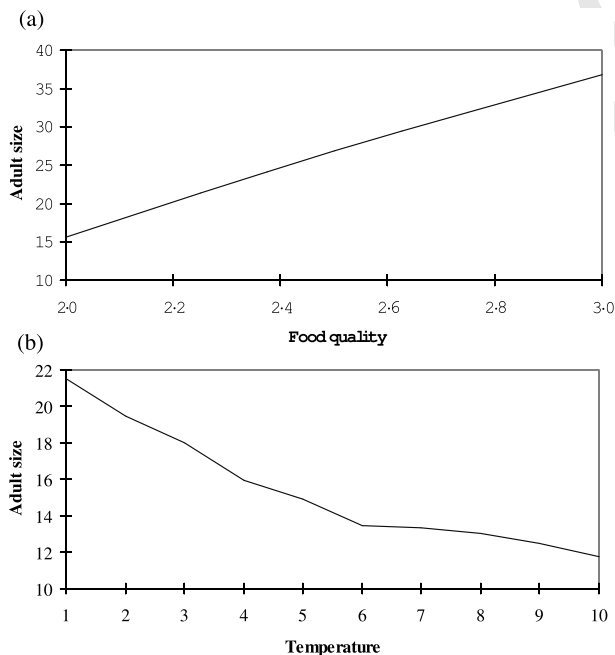ure dependence of body size would evolve. In our model, food quality will affect the assimilation rate, a, but it can hardly be expected to affect the conversion rate, M, or the rate of senescence, d. If this is true, then an increase in food quality results in larger adults [Fig. 4a and (3)]. Temperature, on the contrary, speeds up all the processes and therefore one would expect temperature to affect all these three parameters equally. If this is accepted, then an increase in temperature results in larger or smaller adults, depending on the shape of the senescence function, n (see Fig. 4b and Appendix). These assumptions seem logical and there is some evidence that they are true for aphids (Dixon & Kindlmann, 1994). However, it is likely that the differential response in adult size to changes in food quality and temperature in nature may result from differential responses of our model parameters (a, M and d) to changes in these environmental parameters. This prediction does not require any special type of growth function and probably resolves the 'life history puzzle' (Sevenster, 1995).

The difference between the other optimal energy allocation models and that presented here is the inclusion of senescence as a component, and omission of a negative trade-off between growth rate and mortality and/or a specific growth curve. This novel approach predicts the triangular fecundity function, so characteristic for insects, and contrary to all other models is able to predict a differential effect of food quality and temperature on adult size.

Acknowledgments

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(a)

(b)

Fig. 4 Adult size as a function of: (a) a, ranging from 2 to 3 for $M = 0.65$ and $d = 0.1$; and (b) $a = M = 3d$ and d ranging from 0.5 to 1.

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Appendix

Assume $a(T) = aT$, $M(T) = MT$, $n = n(t, T)$. Thus we get from (3), for $t > D$:

$$g' = n(t, T)TaS^{\alpha}(D) - MTg, \quad g(D) = 0 \quad (A1)$$

with the constraint

$$\int_{D}^{+\infty} g(t, T)MT\, e^{-rt}\, dt = 1. \quad (A2)$$

Integration of (A2) per parts gives

$$MT \int_{D}^{+\infty} e^{-rt} g(t)\, dt$$

$$= \frac{MT^2 aS(D)^{\alpha}}{MT + r} \int_{D}^{+\infty} n(t, T)e^{-rt}\, dt \ (=1). \quad (A3)$$

Denote

$$F(D, r) = \frac{TaS(D)^{\alpha}}{MT + r} \int_{D}^{+\infty} n(t, T)e^{-rt}\, dt - \frac{1}{MT} \equiv 0. \quad (A4)$$

According to the implicit function theorem

$$\frac{dF}{dr}\frac{dr}{dD} + \frac{dF}{dD} \equiv 0. \quad (A5)$$

From (A5):

$$\frac{dr}{dD} = -\frac{(dF/dD)}{(dF/dr)}. \quad (A6)$$

Explicit solution of (3a) by separation of variables yields the solution

$$S(D, T) = \left(TDa(1 - \alpha) + S_0^{1-\alpha}\right)^{1/(1-\alpha)} \quad (A7)$$

and therefore

$$\frac{dS}{dD} = TaS(D, T)^{\alpha}. \quad (A8)$$

Calculating the derivatives gives:

$$\frac{dF}{dD} = \frac{Ta\alpha S(D)^{\alpha-1}(dS/dD)}{r + MT} \int_{D}^{+\infty} n(t, T)e^{-rt}\, dt$$

$$- \frac{TaS(D)^{\alpha}}{r + MT} n(D, T)e^{-rD}$$

$$= \frac{TaS(D)^{\alpha}}{r + MT}$$

$$\times \left(\frac{\alpha Ta}{TDa(1-\alpha) + S_0^{1-\alpha}} \int_{D}^{+\infty} n(t, T)e^{-rt}\, dt - n(D, T)e^{-rD} \right) \quad (A9)$$

and

$$\frac{dF}{dr} = -\frac{TaS(D)^{\alpha}}{r + MT} \left(\frac{1}{r + MT} \int_{D}^{+\infty} n(t, T)e^{-rt}\, dt \right.$$

$$\left. + \int_{D}^{+\infty} tn(t, T)e^{-rt}\, dt \right). \quad (A10)$$

Substituting (A9) for dF/dD and (A10) for dF/dr, respectively, in (A6) gives

$$\mathrm{d}r/\mathrm{d}D = \frac{\alpha Ta/(TDa(1-\alpha)+S_0^{1-\alpha})\int_D^{+\infty} n(t,T)\mathrm{e}^{-rt}\,\mathrm{d}t - n(D,T)\mathrm{e}^{-rD}}{1/(r+MT)\int_D^{+\infty} n(t,T)\mathrm{e}^{-rt}\,\mathrm{d}t + \int_D^{+\infty} tn(t,T)\mathrm{e}^{-rt}\,\mathrm{d}t}$$

(A11)

The denominator of (A11) is always positive and consideration of the signs of the numerator shows that r reaches its maximum, if and only if

$$TD = \frac{\alpha T}{1-\alpha}\frac{\int_D^{+\infty} n(t,T)\mathrm{e}^{-rt}\,\mathrm{d}t}{n(D,T)\mathrm{e}^{-rD}} - \frac{S_0^{1-\alpha}}{a(1-\alpha)}$$

$$= \frac{\alpha T}{(1-\alpha)(\mathrm{d}/\mathrm{d}D)\left(\log \int_D^{+\infty} n(t,T)\mathrm{e}^{-rt}\,\mathrm{d}t\right)} - \frac{S_0^{1-\alpha}}{a(1-\alpha)}$$

(A12)

Substitution for $S_0^{1-\alpha}$ from (A7) into (A12) gives, after some algebra:

$$S(D,T) = \left[\frac{\alpha aT \int_D^{+\infty} n(t,T)\mathrm{e}^{-rt}\,\mathrm{d}t}{n(D,T)\mathrm{e}^{-rD}}\right]^{1/1-\alpha}$$

$$= \left[\frac{\alpha aT}{(\mathrm{d}/\mathrm{d}D)\left(\log \int_D^{+\infty} n(t,T)\mathrm{e}^{-rt}\,\mathrm{d}t\right)}\right]^{1/1-\alpha}$$

(A13)

Thus, it depends on the shape of the $n(D,T)$ function, whether S increases or decreases with T. Figure 4 shows that a decrease is possible.

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