

Behavioural and physiological responses to food availability and predation risk

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ABSTRACT

Several empirical studies have demonstrated the existence of intraspecific variation in age and size at reproductive maturity for organisms experiencing different food environments and predation risk. For some species, these changes have been shown to arise primarily through changes in foraging activity. Theoretically, changes in age and size at maturity can arise through either behavioural or physiological responses. Here we analyse two models. The first is a conventional life-history model with no explicit recognition of the physiology of energy utilization by the organism – growth (i.e. weight gain) is simply the difference between assimilation and respiration, and there are no physiological restrictions on the timing of maturation. The changes in age and size at maturity in response to food availability and predation risk predicted by this model are consistent with published experimental data for one particular species, the midge *Chironomus tentans*. Numerical calculations with parameters appropriate to this species suggest that the optimal response is purely behavioural. The second model is a general, dynamic energy budget model that takes account of the energetic costs associated with development to reproductive maturity. With that model, we prove that the optimum partitioning of energy between growth and development is independent of predation risk and food availability, thereby demonstrating the generality of the previous finding with the life-history model. On the basis of the combined insight from the two models, we propose that fixed allocation to growth and development, despite variation in food availability and predation risk, is optimal for a broad class of life histories. Consequently, the absence of an allocation response to experimental manipulation of food or predators should not necessarily be taken as evidence for physiological or other constraints on life-history adaptation.

Keywords: age at maturity, Chironomidae, foraging activity, growth curve, life history, optimization, resource allocation, size at maturity.

INTRODUCTION

A central theme of life-history theory and behavioural ecology is the study of trade-offs (Stearns, 1989). By manipulating the costs and benefits of the different options available to an

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organism and observing its response, it is possible to determine whether an organism's solution to a trade-off is adaptive. One of the most commonly studied trade-offs faced by an animal is that growing larger and more fecund is often associated with increased risk of predation before maturation (Roff, 1992; Stearns, 1992). Although there is a large body of theory to predict responses to changes in food availability and predation risk (Roff, 1981; Stearns and Koella, 1986; Kozlowski, 1992; Bernardo, 1993; Houston *et al.*, 1993; Abrams *et al.*, 1996; Abrams and Rowe, 1996), relatively little attention has been paid to the mechanisms underlying these responses (Skelly and Werner, 1990; Ball and Baker, 1996).

Two general types of mechanisms can be distinguished, which we term 'behavioural' and 'physiological' responses. A behavioural response is a change in foraging activity, such as refuge use or movement, which influences predation risk as well as food acquisition (Lima and Dill, 1990). Typically, such responses can be directly observed in an experiment (e.g. Sih, 1986; Gilliam and Fraser, 1987; Macchiusi and Baker, 1991, 1992; Werner and Anholt, 1993; Peckarsky and McIntosh, 1998). For a given food density, decreasing foraging activity reduces ingestion rate and hence growth rate. If maturity occurs at a fixed size, a pure behavioural response leads to an increase in age at maturity.

A physiological response is a response that does not involve any variation in foraging activity or ingestion rate (Ball and Baker, 1996). An important example is a change in the proportion of assimilated energy allocated to growth versus development. By development we mean those processes and tissues to which some fixed amount of assimilate must be dedicated, regardless of the state of the environment, in order to reach reproductive maturity. For a given ingestion rate, increasing allocation to development decreases maturation time at the expense of smaller size at maturity.

Life-history variation induced by changes in food availability or predation risk can, in principle, involve either one or both types of response, and it may be difficult to infer the mechanism operating in any particular study from observable life-history variables. Ball and Baker (1996; see also Skelly and Werner, 1990) proposed a technique to isolate physiological from behavioural responses in empirical life history data, and applied this technique to their data from experiments with sunfish preying on larvae of the aquatic midge *Chironomus tentans*. They found no evidence of a physiological response to increasing predation risk. This result can be interpreted in two ways: either there are physiological constraints on potentially adaptive life-history plasticity in *C. tentans*, or a purely behavioural response is optimal.

In this paper we ask whether the optimal response to changes in food availability and predation risk includes a physiological as well as a behavioural response. We address this question using two theoretical approaches. First, we construct a conventional life-history model with no explicit representation of the energetic costs of development. We use this model to calculate the optimal level of foraging activity, and age and size at maturity, as functions of food availability and predation risk. We rearrange the output of this model to determine the mechanism underlying the predicted life-history shifts. Numerical calculations with parameters appropriate to the midge *C. tentans* studied by Ball and Baker (1996) suggest that the optimal response is purely behavioural. Second, we construct a dynamic energy budget model, with explicit representation of allocation to growth and development. With this model, we assess the optimal physiological response directly, and show analytically that it is independent of food and predation risk.

Models to predict optimal age and size at maturity have a long history in life-history theory (e.g. Kozlowski, 1992; Roff, 1992; Stearns, 1992); more recent theory has incorporated adaptive variation in foraging effort (Abrams *et al.*, 1996; Abrams and Rowe, 1996). No single, general result has

emerged; indeed, analysis of the most general models has shown that any qualitative response to variation in predation risk and food availability is possible, depending on the particular expressions used for the growth curve, the relationship between predation rate and foraging activity, and other model functions. To make predictions for a particular species, one must specify the shapes of at least some of these functions (Abrams *et al.*, 1996; Abrams and Rowe, 1996). Furthermore, the appropriate forms of these functions, and even the appropriate fitness measure, are subjects of considerable debate (Alford and Jackson, 1993; Mylius and Diekmann, 1995; Day and Taylor, 1997; Brommer, 2000).

This raises challenging questions about generality. Although our first model took minimal account of physiology, the assumptions about the size-dependence of growth rate were sufficiently specific to allow us to simulate Ball and Baker's (1996) data for *C. tentans*. Thus, while addressing the issue of optimal mechanisms, we also evaluated the ability of a simple model to predict life-history responses in a particular system. The case for generality of the results in the present paper rests on combining the numerical findings from the life-history model with the more general analysis that is possible with the second (dynamic energy budget) model. Because the results of the two models are consistent, we predict that adaptive changes in life history in response to the environment experienced by juveniles involve only behavioural responses for a broad class of life histories.

LIFE-HISTORY OPTIMIZATION MODEL

For our first approach, we construct an optimization model guided by the life history and foraging behaviour of *C. tentans*. The aquatic larvae of *C. tentans* construct tubes composed of substrate particles tied together with salivary secretions. While inside the tube, a larva is relatively invulnerable (or inconspicuous) to visual predators; however, it must extend its head and part of its thorax and abdomen to graze on substrata. Growth ceases at maturity, and adults do not feed. Hence, fecundity, which depends on adult size, is limited by foraging during the larval stage. The short-lived adult females typically produce a single egg cluster soon after mating.

We define foraging activity (a) as the fraction of time spent foraging outside the larval tube. Size at maturity is a function of foraging activity and age at maturity (T). We calculate the optimal foraging activity and age at maturity over a range of food levels and predation risk by maximizing fitness with respect to a and T . For this model, we assume that the individual has the behavioural and physiological flexibility to achieve the optimum. More specifically, given the ingestion rate determined by the optimal foraging activity for a particular food level and predation risk, the individual must be able to finish development in the corresponding optimal time to maturation.

Life-history framework

The first step in any optimization model is to select a fitness measure. The most generally appropriate fitness measure is non-invasibility (Metz *et al.*, 1992), which requires specification of the environmental feedback that regulates a population. Two obvious candidates for the source of this feedback are resource competition and predation, but we have no evidence for particular regulatory mechanisms occurring in the life history of *C. tentans*. Under certain simplifying assumptions, however, one of the two commonly applied density-independent fitness measures, the intrinsic rate of increase (r) and lifetime reproduction (R_0), is

maximized by selection for non-invasibility (Charlesworth, 1994; Mylius and Diekmann, 1995). For the subsequent analysis, we use r , which is theoretically justified when density dependence affects the mortality rate of all age classes equally.

The value of r is the solution to the Euler-Lotka equation (Charlesworth, 1994):

$$\int_0^{\infty} e^{-rt} l_t m_t dt = 1 \quad (1)$$

where t is age, l_t is the probability of survival to age t , and m_t is the birth rate at age t .

We first simplify equation (1) as much as possible before specifying the dependence of growth and mortality on foraging activity. We assume that the optimal age at maturity is not influenced by time constraints. Larval development time in *C. tentans* can vary by approximately 50% (Ball and Baker, 1996), suggesting that, for example, synchronous emergence is not important. Furthermore, the short generation time, which potentially allows multiple generations per year, suggests that ignoring seasonality is a reasonable simplification in our model.

For organisms that do not grow after reaching the adult stage, we assume that m_t is independent of age for $t > T$, where T is the age at maturity. Fecundity is then some function Φ of length at maturity, L_T , so

$$m_t = \begin{cases} 0 & t < T \\ \Phi(L_T) & t \geq T \end{cases} \quad (2)$$

We denote the larval mortality rate by μ_l , which is assumed to be independent of the size of a larva. If the adult mortality rate, μ_a , is independent of age and size at maturity, then

$$l_t = \begin{cases} e^{-\mu_l t} & t < T \\ e^{-\mu_l T} e^{-\mu_a(t-T)} & t \geq T \end{cases} \quad (3)$$

Substituting from equations (2) and (3) into equation (1), and evaluating the integral, we obtain

$$\Phi(L_T) \frac{e^{-(r+\mu_l)T}}{r+\mu_a} = 1 \quad (4)$$

This equation cannot be solved analytically for r . In the following section, we define functions for Φ , L_T and μ_l in order to proceed with the optimization.

Growth, fecundity and mortality

We model growth with a simple power function, which gives a reasonable fit to empirical data from *C. tentans* (Ostrovsky, 1995). The rate of change in mass is equal to the net production (assimilation – maintenance), which is proportional to mass raised to the power h :

$$\frac{dW}{dt} = g W^h \quad (5)$$

where

$$g = \varepsilon \xi A(a) f - \gamma \quad (6)$$

In equation (6), ε is the conversion efficiency, ξ is the maximum ingestion rate (scaled to W^h) and γ is the maintenance rate. $A(a)$ is a dimensionless function relating maximum ingestion

rate to foraging activity. The scaled functional response, f , is the fraction of the maximum possible ingestion rate that an individual achieves at a given food density. The functional response can take a variety of forms (e.g. type I, II or III), but must increase with food density. Rather than specify its shape, we use f as the measure of the food level in the environment.

We further assume that net production is proportional to surface area ($h = 2/3$), consistent with chironomid data summarized by Ostrovsky (1995). Equation (5) can then be rewritten in terms of length (L):

$$\frac{dL}{dt} = \frac{g}{3\chi^{1/3}} \quad (7)$$

where χ is an allometric parameter relating length and mass ($W = \chi L^3$). Hence, if initial length is L_0 ,

$$L_T = \frac{g^T}{3\chi^{1/3}} + L_0 \quad (8)$$

Fecundity in *C. tentans* is an approximately linear function of length (see Appendix), so we write

$$\Phi(L_T) = aL_T + b \quad (9)$$

where $a > 0$. The parameter b can in theory be positive or negative, but it will in general be negative if a minimum size is necessary for reproduction.

We assume that the larval mortality rate is the sum of background mortality (μ_b) and predation mortality:

$$\mu_l = \mu_b + pM(a) \quad (10)$$

where $M(a)$ is a function relating predation rate to foraging activity, and p is a combination of predator density and a coefficient which converts this term to the predation rate.

Finally, we specify functions for $A(a)$ and $M(a)$. Data for these functions are scarce for any species, presumably because it is difficult to manipulate foraging activity directly. In this paper, we use the functions $A(a) = a^c$ and $M(a) = a^d$. These simple functions can take a variety of shapes from concave to convex, depending on the values of the parameters c and d .

Optimization

Having defined the necessary functions, we now find the optimal combination of foraging activity and age at maturity by maximizing the fitness measure (r) with respect to each of these variables. Although we could not obtain an explicit expression for r from equation (4), we can derive conditions for the optimum by implicit differentiation of equation (4) with respect to a and T . The result is three equations,

$$\Phi(L_T) \frac{e^{-(r + \mu_l)T}}{r + \mu_a} = 1 \quad (11)$$

$$\frac{\partial \Phi}{\partial T} - \Phi(L_T)(r + \mu_l) = 0 \quad (12)$$

$$\frac{\partial \Phi}{\partial a} - \Phi(L_T)T \frac{\partial \mu_1}{\partial a} = 0 \quad (13)$$

and three unknowns: r , a and T . Equations (11–13) cannot be solved analytically for optimal a and T . Instead, we search for numerical solutions of the parameterized model.

We parameterized the model for *C. tentans* with published empirical data. The details of the parameterization are provided in the Appendix, and the resulting values are listed in Table 1. Because data for some parameters were unavailable, we approximated ξ and γ as the midpoint of the possible range of values.

The parameters c and d determine the shape of the functions relating ingestion and predation to activity. Both c and d must be positive because ingestion and predation rates increase with activity. In the absence of any other relationship between ingestion and foraging activity, the ingestion rate is simply proportional to time spent foraging (i.e. $c = 1$). Although we do not have any direct evidence for the shape of the predation function, we hypothesize that $M(a)$ is accelerating. Our reasoning is that predators may notice individual prey that spend long periods of time outside the larval tube, resulting in a predation rate that increases non-linearly with activity. The value of d listed in Table 1 merely serves as a starting point for numerical analysis, in which we allow $A(a)$ and $M(a)$ to vary from decelerating to accelerating.

Although *C. tentans* is effectively semelparous, our assumption of constant birth and adult mortality rates implies continuous reproduction during the adult stage. In our numerical calculations, we found that a model with an adult stage duration that is short relative to the larval stage duration gives results that are qualitatively equivalent to the predictions from a model of strictly semelparous organisms. Keeping the adult stage in the model allows us to vary its duration to explore the effects of adult life span on our results.

The predictions of the parameterized model are plotted in Fig. 1a–c. In Fig. 1d–f, we have plotted data from Ball and Baker (1996) and Macchiusi and Baker (1992) for comparison. These data were not used in the parameterization. We were unable to completely parameterize the model, so we cannot make quantitative predictions for *C. tentans*. However, we note that the model predictions for age and length at maturity fall within the naturally observed range.

Table 1. Parameter values for the life-history model (for details and sources, see the Appendix)

Parameter	Value	Description
a	$45 \text{ eggs} \cdot \text{mm}^{-1} \cdot \text{day}^{-1}$	coefficient in length–fecundity relationship
b	$-397 \text{ eggs} \cdot \text{day}^{-1}$	intercept in length–fecundity relationship
c	1	exponent in ingestion–activity function
d	2	exponent in predation–activity function
γ	$0.1 \text{ mg}^{1/3} \cdot \text{day}^{-1}$	maintenance rate
L_0	0.1 mm	length at birth
ξ	$16 \text{ mg} \cdot \text{day}^{-1} \cdot \text{mg}^{-2/3}$	maximum ingestion rate
μ_a	$0.5 \cdot \text{day}^{-1}$	adult mortality rate
μ_b	$0.005 \cdot \text{day}^{-1}$	larval background mortality rate

Furthermore, the qualitative predictions of the model for age at maturity match the patterns in Ball and Baker's (1996) data. Specifically, age at maturity increases with predation risk and decreases with food level. The match between model predictions and data for length at maturity is mixed. As predicted, length at maturity decreases with predation risk, but the effect is extremely small at medium food level. Length at maturity increases with food level in the absence of predators, but is unaffected by food level when predators are present. The model predicts a relatively small increase in length at maturity with food regardless of predation risk.

The model correctly predicts the reduction in foraging activity with increasing predation risk in the data from Macchiusi and Baker (1992). However, in the experimental data, foraging activity increases with food level when predators are present, but decreases with food level in the absence of predators. We address this mismatch between theory and observation in the Discussion.

Given the uncertainty of our parameter estimates, we wished to establish whether the qualitative predictions of the model are robust to changes in the parameter values that we used to calculate the optima. In particular, we have the least confidence in the values of the parameters which define the growth curve (ξ , γ) and the exponents in the activity functions (c , d). We conducted a numerical search, varying ξ , γ , c and d over two orders of magnitude around our original estimates, but we were unable to find a combination of values for which the qualitative predictions differed from those in Fig. 1. Thus, the model predictions appear to be robust to substantial variation in the parameters.

Behavioural versus physiological response to the environment

While the results presented above show that the qualitative patterns in age and size at maturity are consistent with the empirical data, we have not yet addressed the question of whether the life-history responses result from changes in allocation in addition to changes in foraging activity. We now consider this question using the analysis described by Ball and Baker (1996). We outline the general argument and then manipulate the optimization model output from the previous section to determine whether the optimal response includes an allocation shift.

Detection of an allocation shift is illustrated in Fig. 2a. At a given predator density, growth and development are expected to be positively correlated over a range of food density. In the absence of any change in allocation with increasing predation risk, decreasing foraging activity is equivalent to decreasing food density in its effect on growth and development rates (moving down and to the left on a single line in Fig. 2a). Alternatively, if individuals increase allocation to development as predation risk increases, treatments with different predation risk fall on distinct lines. For instance, for a given growth rate, individuals from high predation risk treatments might have a higher development rate. This argument is quite general, and does not depend on the details of the allocation process.

Ball and Baker (1996) applied this technique to their data from *C. tentans*, which we have reproduced in Fig. 2b. They found no significant difference in development rates between predator and no-predator treatments after correcting for variation in growth rates. Hence, they concluded that, in the absence of evidence for a physiological response, the variation must be solely due to the behavioural response.

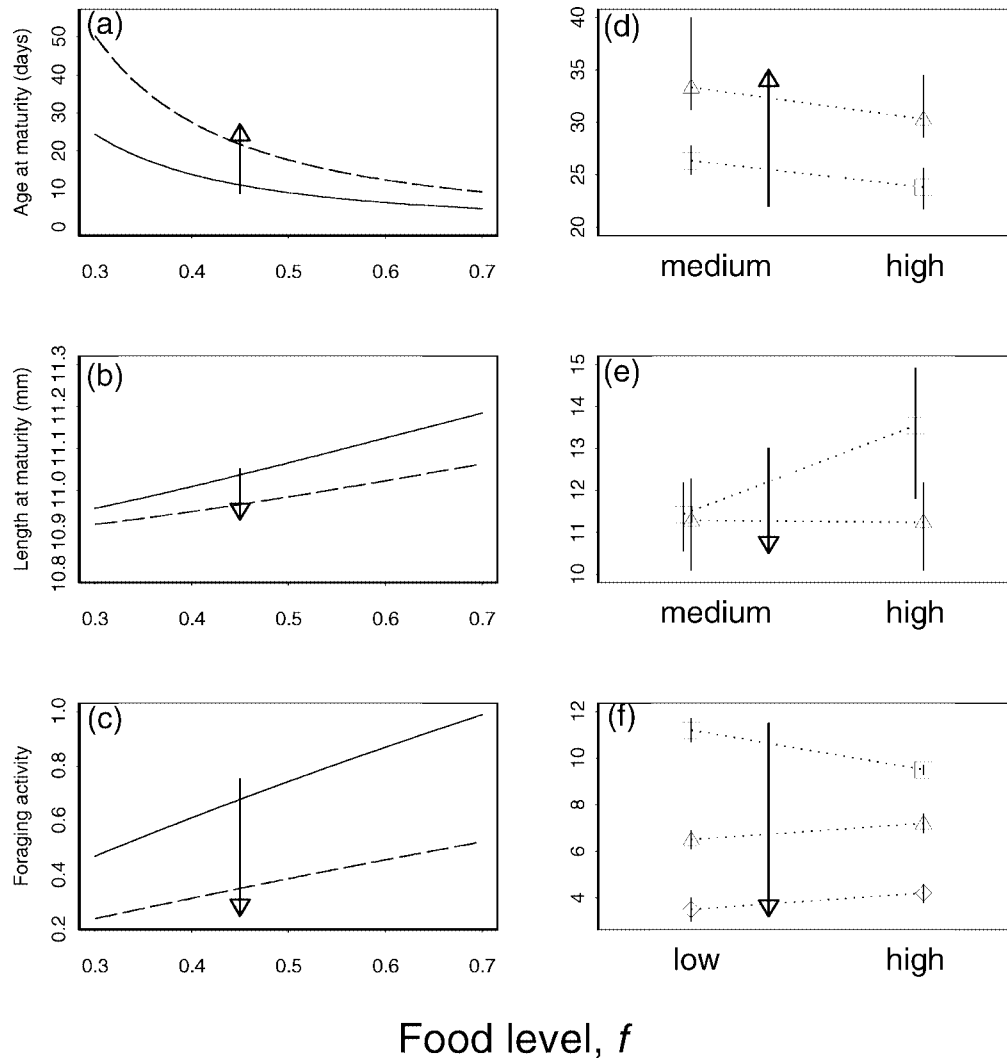


Fig. 1. (a–c) Life-history optimization model predictions for two predation levels (see equation 10): $p = 0.5 \cdot \text{day}^{-1}$ (solid line) and $p = 1 \cdot \text{day}^{-1}$ (dashed line). (d) Medians and inter-quartile ranges for females from Ball and Baker (1996). Treatments with no predators are labelled with squares, and treatments with predators are labelled with triangles. (e) Means and standard deviations for females from Ball and Baker (1996), converted from dry mass (see Appendix). Symbols as in (d). Points for each treatment are offset for clarity. The apparent interaction between the effects of food level and predation risk was not statistically significant (Ball and Baker, 1996). (f) Data from Macchiusi and Baker (1992). Foraging activity is measured as the number of larvae moving, out of 20 in each treatment, on the last day of a 7 day experiment. Symbols are as in (d), but triangles and diamonds represent low and high predator levels, respectively. Low predator level = predator present 20% of each day of the experiment. High predator level = predator present 100% of each day. Food level treatments consisted of addition of different volumes of a suspension of finely ground fish food. Ball and Baker (1996) used three food levels, but did not report data from the lowest, due to poor survival. Macchiusi and Baker (1992) used two food levels, which are not equal to the levels in (d) and (e). Arrows indicate increasing predation risk.

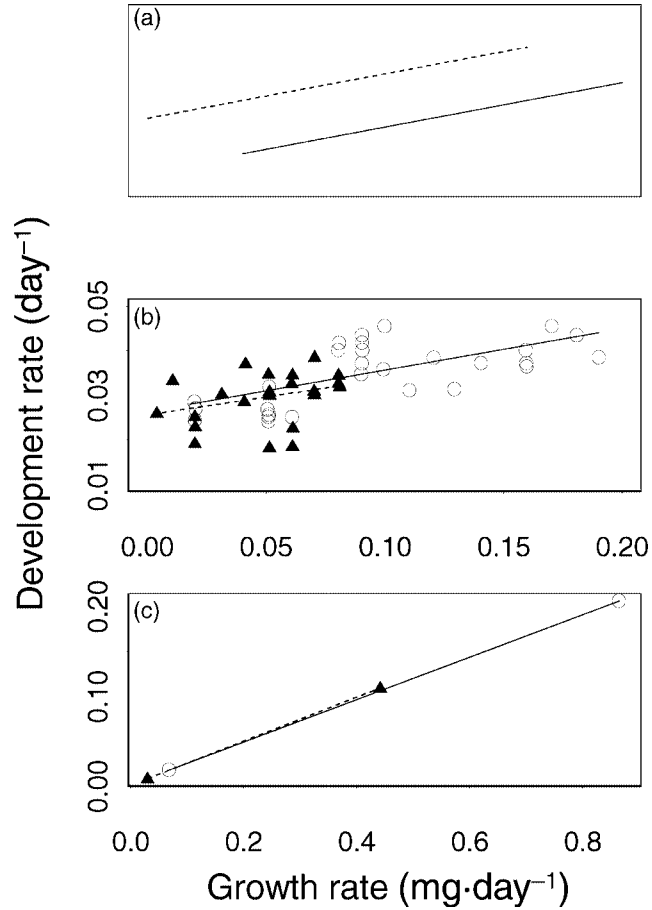


Fig. 2. (a) Predictions from Ball and Baker (1996). The solid line represents low predation treatments, and the dashed line represents high predation treatments. (b) Data for females from Ball and Baker (1996) for no-predator treatments (○) and predator treatments (▲). Each point represents one replicate of the medium or high food level (as in Fig. 1d,e). Development rate is the inverse of age at emergence. Growth rate is measured as the average over 5 day intervals. Slopes and intercepts of regression lines for treatments without predators (solid line) and with predators (dashed line) are not significantly different. (c) Predictions from the optimization model. Because the lines overlap, we have placed circles at the endpoints of the curve calculated with $p = 0.5 \cdot \text{day}^{-1}$ and triangles at the endpoints of the curve calculated with $p = 1 \cdot \text{day}^{-1}$. Growth rate is measured as length divided by age at maturity.

To determine whether a purely behavioural response is optimal, we rearrange the output of our life-history model to match the variables in Fig. 2a. Development rate is simply the inverse of age at maturity, $1/T$. We use average growth rate during the larval stage from our growth model, $(W_T - W_0)/T$, where W_0 is mass at birth. The results from our optimization model are displayed in Fig. 2c. Despite doubling the predation rate, the model predicts a virtually undetectable change in allocation, consistent with Ball and Baker's (1996) empirical results.

ALLOCATION MODEL

The life-history optimization model in the previous section suggests an adaptive explanation for the responses of *C. tentans* to changes in food availability and predation risk. To assess the generality of our results, we reinterpret Ball and Baker's (1996) verbal model in terms of a simple energy allocation model. We retain the assimilation and mortality functions from the previous section, but we introduce an explicit representation of the partitioning of assimilate between growth and development. Hence, age and size at maturity are now functions of foraging activity and the relative allocation to development versus growth.

The allocation model depends on two key assumptions. First, we assume the simplest possible partitioning rule: a constant fraction θ of assimilated food is allocated to growth, and the remaining fraction $(1 - \theta)$ is used for development. Second, we assume that maturation occurs when some fixed total quantity D of assimilate has been allocated to development. This assumption represents the energetic constraint on maturation that was absent from the model in the previous section.

Constant θ is presumably a simplification of the allocation process. However, Kooijman (2000) argues that partitioning between growth and development occurs at the cellular level of energy uptake from transport tissue. For cells involved in development to increase their relative uptake (i.e. decrease θ) during the larval stage, other cells must reduce their uptake. Because individual cells do not have information about uptake by other cells, coordination at this level is unlikely. Furthermore, large changes in θ during the larval stage would result in noticeable variation in the larval growth rate. For instance, a shift from growth to development would produce a sudden deceleration in the latter portion of the larval growth curve. Empirical evidence shows that chironomid larvae continue to grow through most of the final larval instar (e.g. Ineichen *et al.*, 1979), suggesting that constant θ is a reasonable approximation.

These assumptions result in the following equations for growth and development:

$$\frac{dW}{dt} = \theta g W^h \quad (14)$$

$$\frac{dQ}{dt} = (1 - \theta)g W^h \quad (15)$$

where Q is the quantity of assimilate allocated to development. From equations (14) and (15), we immediately see that the relationship between development rate and growth rate is

$$\frac{dQ}{dt} = \left(\frac{1 - \theta}{\theta} \right) \frac{dW}{dt} \quad (16)$$

which is directly comparable with Ball and Baker's (1996) verbal model (Fig. 2a).

As food density increases, both development rate and growth rate increase, and for a given value of θ the relationship is linear (equation 16). If θ is hypothesized to decrease with increasing predator density, development rate at the higher predator density increases for any given food density (Fig. 3). In contrast to Ball and Baker's (1996) verbal model, equation (16) predicts that the slope also increases with predator density. Nevertheless, these results are still consistent with the interpretation of the lack of a difference between the regressions of growth rate on development rate as an absence of variation in θ .

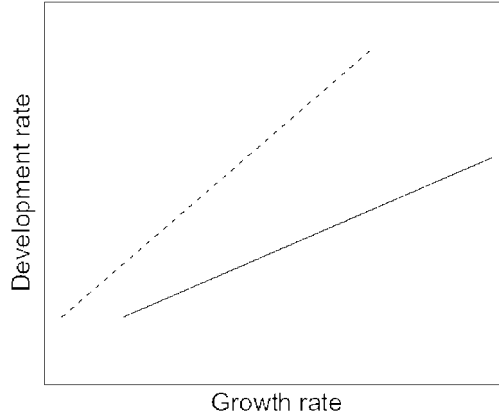


Fig. 3. Allocation model predictions for low allocation to development relative to growth (high θ , solid line) and high allocation to development relative to growth (low θ , dashed line).

To determine optimal allocation, we require solutions for T and W_T from equations (14) and (15). First, we solve equation (14) for W_t :

$$W_t = (\theta g(1-h)t + W_0^{1-h})^{1/(1-h)} \quad (17)$$

Next, assuming W_0 is negligible,

$$Q_t = g(1-h)(1-\theta)(\theta g(1-h))^{h/(1-h)} t^{1/(1-h)} \quad (18)$$

Given the energetic constraint on development, time to maturation (T) is simply the time required to accumulate D units of assimilate for development. Setting $Q_T = D$ and solving equation (18) for T results in

$$T = \left(\frac{D}{g(1-h)(1-\theta)} \right)^{1-h} (\theta g(1-h))^{-h} \quad (19)$$

Setting $t = T$ in equation (17) and substituting equation (19), we obtain an expression for mass at maturity:

$$W_T = \frac{D\theta}{1-\theta} \quad (20)$$

Next, we insert the allocation model into the life-history optimization framework used above. Because the adult life span of *C. tentans* is short relative to the larval stage duration and adult females typically produce only one cluster of eggs (Townsend *et al.*, 1981), we simplify the life-history model by assuming semelparity. In this case,

$$r = \frac{\ln[\Phi(L_T)]}{T} - \mu_1 \quad (21)$$

and we maximize r with respect to θ .

Setting the derivative of r with respect to θ equal to 0 and substituting from equation (19) gives

$$(\Phi(L_T)\theta^h(1-\theta)^{1-h})^{-1} \frac{d\Phi(L_T)}{d\theta} + \ln[\Phi(L_T)](h\theta^{-(h+1)}(1-\theta)^{h-1} + (h-1)\theta^{-h}(1-\theta)^{h-2}) = 0 \quad (22)$$

Solving equation (22) for θ would give optimal allocation as a function of predation risk, p . However, p appears only in μ_i or possibly the optimal value of a , neither of which appears in W_T (equation 20). Given our assumption that L_T is related to W_T by an allometric function, L_T and therefore $\Phi(L_T)$ are independent of predation risk. Similarly, no other term in equation (22) depends on p . Hence, we do not need to simplify equation (22) further to conclude that the optimal response to variation in predation risk does not involve a change in allocation to development relative to growth.

The result of the allocation model can be explained intuitively as follows. Increasing predation affects fitness only through mortality, which influences the optimal foraging activity. Changing a alters ingestion (changing g in equations 14–15), but does not affect the relative rates of growth and development (equation 16). Hence, the optimal allocation to growth versus development does not vary with predation risk.

DISCUSSION

We applied two complementary approaches to determine optimal foraging behaviour and allocation to growth and development. In the life-history model presented first, the optimization variables are identical to the quantities measured by Ball and Baker (1996) in *C. tentans*. This correspondence allowed a direct comparison of our model results with their experimental analysis, so we could verify the predictions of the parameterized model with independent empirical data. However, the generality of the first model is uncertain because it is analytically intractable. We analysed optimal allocation more directly with the second model. In this case, the physiological response is represented explicitly, and we demonstrated analytically that optimal allocation is independent of predation risk.

Our analysis of behavioural and physiological responses to increased predation risk shows that the absence of an allocation shift does not necessarily indicate that organisms are unable to make such a change. Furthermore, the invocation of other, unknown processes or selective forces is not necessary to explain results such as those reported by Ball and Baker (1996). For instance, Ball and Baker (1996) hypothesize that competition among *C. tentans* larvae may select for early oviposition by adult females. In this scenario, relative allocation to development may remain at its physiological maximum, thereby precluding the possibility of any change with predation risk. Alternatively, the physiological mechanisms by which resources are partitioned within an individual may be inflexible. However, we suggest that in species such as *C. tentans* with life histories in the general category encompassed by our models, fixed allocation is the optimal response to increasing predation risk.

The verbal model proposed by Ball and Baker (1996) does not consider changes in allocation in response to variation in food density. In terms of Fig. 2a, increasing allocation to growth relative to development with increasing food density would result in decelerating, concave-down curves. Conversely, increasing allocation to development with food would result in accelerating curves. Our allocation model predicts that θ is independent of food as

well as predator density (equation 22). Similarly, the parameterized optimization model predicts no allocation shift in response to food. However, the data plotted in Fig. 2b hint at a deceleration of the curve relating development rate to growth rate, indicating that allocation to growth may increase slightly with food density. Alternatively, the apparent plateau in the data might be the result of physiological constraints on maximum growth and development rates. If development reaches its maximum rate at a lower food density than growth, Ball and Baker's (1996) high food/no predator treatment might have been sufficient to generate this saturation effect.

Despite uncertainty in the parameterization of the growth function and the form of the behaviour functions in the optimization model, the qualitative predictions for age and length at maturity were consistent with experimental data from Ball and Baker (1996). The congruence between model results and data for foraging activity is less clear. Although our model correctly predicts the response to predation, the data for the response to food do not follow the same pattern across predator treatments (Fig. 1f). We interpret this discrepancy as a result of the simplicity of our model of foraging activity. In the data from Macchiusi and Baker (1992), the lowest predation risk treatment is the complete absence of predators. According to our model, the optimal behaviour in the absence of predators is maximum foraging activity ($a = 1$). For real chironomids, the absence of predators may allow behavioural processes that we have not considered, such as tube maintenance, to become increasingly important in determining time spent inside and outside the tube. Furthermore, Macchiusi and Baker (1992) found that the response of foraging activity to food level depends on the duration of the experiment as well as the presence or absence of light. In our model, a represents the average foraging activity over the larval stage, whereas Macchiusi and Baker (1992) measured activity over relatively short periods. Consideration of variation in foraging behaviour at a short time-scale might be required to improve the predictions of our model. Further empirical work on the effects of foraging activity on ingestion and mortality would also permit more quantitative tests of the theory.

The life history of *C. tentans* is particularly well suited to the study of anti-predator adaptations. Unlike many of the species that have been studied elsewhere in the literature and for which a substantial body of theory has been developed, such as amphibians (Werner, 1986), *C. tentans* is effectively semelparous and does not grow or feed to produce more eggs after maturation. These life-history features eliminate the possibility of compensation for variation in growth during the larval stage with growth during the adult stage. Hence, we can describe the entire life history in a single, relatively simple model that includes the effects of foraging activity. On the other hand, maturation in *C. tentans* does not appear to be strongly influenced by age, size or, most importantly, seasonal constraints, as is the case in many other insects for which theory exists in the literature (e.g. Abrams *et al.*, 1996).

Our theoretical analysis, however, suggests that the allocation result can be generalized beyond *C. tentans*. Semelparity makes the allocation model analytically tractable, but our first model, which assumes iteroparity, also predicts that allocation does not depend on predation risk. Although our parameterization for *C. tentans* implies a short adult life span, the results suggest that the prediction is not limited to strictly semelparous species. Moreover, our analytic results from the allocation model are independent of the shape of the functions $A(a)$ and $M(a)$, in which we had the least confidence. Hence, we expect the model results to apply to taxa such as many insect species in which growth ceases at maturation and adults have short life spans.

We hypothesize that optimal allocation will vary with predation risk in species in which some of our other assumptions are violated. For instance, the ability to grow after maturity might make rapid maturation at small size in response to increasing predation risk less costly than lower foraging activity at the expense of longer development time. Similarly, seasonal or other time constraints, or size-dependent predation, might provide additional benefits to increasing allocation to development relative to growth with increasing predation risk. These hypotheses suggest further theoretical and experimental work to identify the conditions under which behavioural and physiological responses occur.

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APPENDIX: PARAMETERIZATION

Growth parameters

In the derivation of the growth model for *C. tentans*, we assumed that mass is proportional to length cubed. We do not have data for *C. tentans*, but Ostrovsky (1983, cited in Ostrovsky, 1995) obtained the relationship

$$W = 0.0051L^{2.82}$$

(where W is measured in units of mg wet mass, and L in mm) for the congener, *C. plumosus*. We assume that allometric parameters such as χ are, in general, approximately equal in closely related species. For our model of *C. tentans*, we round off 2.82 to 3, and set the constant of proportionality, χ , to $0.003 \text{ mg} \cdot \text{mm}^{-3}$. This value gives a curve approximately equal to the allometric function found by Ostrovsky (1995) over the range of lengths observed for *C. tentans* larvae. This parameterization is also consistent with data from several species of Chironomidae (Mackey, 1977).

To convert wet mass to dry mass, we used the relationship

$$\text{wet mass} = 5.6 \text{ dry mass}$$

from Townsend *et al.* (1981).

The ingestion rate (I) is

$$I = \xi W^{2/3} f A(a) \quad (\text{A1})$$

Johannsson (1980) determined values for I from *in situ* experiments with *C. plumosus* at 10 different times over the course of a year. Johannsson (1980) also reported average dry masses of the individuals in this experiment. Johannsson (1980) did not measure $A(a)$ or f in these experiments. By definition, each of these quantities, and therefore their product, must be between 0 and 1. As a starting point for our analysis, we set $A(a)f = 0.5$, substitute it into equation (A1), and solve for ξ . We use an average value of approximately $\xi = 16 \text{ mg} \cdot \text{day}^{-1} \cdot \text{mg}^{-2/3}$.

In the same set of experiments, Johannsson (1980) measured the assimilation efficiency, ε , and found values that ranged from 0 to 0.142. Because the quality of natural food is probably lower than the quality of food used in Ball and Baker's (1996) experiments, we take a value from the upper end of the range, $\varepsilon = 0.1$.

Without data for *C. tentans* growth curves, we cannot accurately estimate the maintenance rate, γ . As a first, rough approximation, we substitute the values for ε and ξ determined above into the growth equation and find the value of γ so that age and size at maturity fall within the range of data from Townsend *et al.* (1981), using their values for L_0 . This gives an estimate of $\gamma = 0.1 \text{ mg}^{1/3} \cdot \text{day}^{-1}$.

Length–fecundity relationship

Sibley *et al.* (1997) measured the dependence of adult female fecundity on larval dry mass. We converted larval dry mass to length using the functions specified above, and fit a linear regression to their data with slope = $90 \text{ eggs} \cdot \text{mm}^{-1}$ and intercept = -794 eggs . In our model, we assumed continuous reproduction during the adult stage. Hence, we divided slope and intercept by 2 days, the average adult life span (see below), to obtain $a = 45 \text{ eggs} \cdot \text{mm}^{-1} \cdot \text{day}^{-1}$ and $b = -397 \text{ eggs} \cdot \text{day}^{-1}$, which are the slope and intercept of the length–fecundity relationship used in our model.

Larval and adult mortality

We obtained a value for the background larval mortality rate, μ_b , from Sibley *et al.* (1997). Their data from laboratory experiments conducted over a range of food supplies indicate a reasonably low, average value of approximately 0.005 day^{-1} . We do not have data for adult mortality directly relevant to the analysis. Unmated adult female *C. tentans* can live for approximately a week in the laboratory (personal observation), but upon insemination typically produce only one clutch of eggs before death (Townsend *et al.*, 1981). For our model, we let $\mu_a = 0.5 \cdot \text{day}^{-1}$, which gives an average adult life span of 2 days.