Adaptive significance of critical weight for metamorphosis in holometabolous insects

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ARTICLE INFO

ABSTRACT

Holometabolous insect larvae become committed to metamorphosis when they reach a critical weight. Although the physiological mechanisms involved in this process have been well-studied, the adaptive significance of the critical weight remains unclear. Here, we developed a life history model for holometabolous insects and evaluated it from the viewpoint of optimal energy allocation. We found that, without a priori assumptions about critical weight, the optimal growth schedule is always biphasic: larval tissues grow predominately until they reach a certain threshold, after which the imaginal tissues begin rapid growth, suggesting that the emergence of a critical weight as a phase-transition point is a natural consequence of optimal growth scheduling. Our model predicts the optimal timing of critical-weight attainment, in agreement with observations in phylogenetically-distinct species. Furthermore, it also predicts the scaling of growth scheduling against environmental change, i.e., the relative value and timing of the critical weight should be constant, thus providing a general interpretation of observed phenotypic plasticity. This scaling relationship allows the classification of adaptive responses in critical weight into five possible types that reflect the ecological features of focal insects. In this manner, our theory and its consistency with experimental observations demonstrate the adaptive significance of critical weight.

1. Introduction

The determination of organism size is both an old and new problem in developmental biology. Although the approximate size of each species is genetically pre-determined, individual size varies depending on nutrition, temperature and/or other rearing conditions (Nylin and Gotthard, 1998). The genetics and physiology of developmental programs involved in size-determination have been well-studied, especially for holometabolous insects (Edgar, 2006; Mirth and Riddiford, 2007).

In holometabolous insects, size-determination is closely related to metamorphosis as insects cease growing prior to metamorphosis. It has long been known that a larva becomes committed to metamorphosis when it reaches a critical weight (CW) (Nijhout et al., 2014; Yamanaka et al., 2013). CW is experimentally defined as the larval weight at the point in larval development after which starvation no longer delays the onset of metamorphosis, and is considered to be a developmental switch for metamorphosis. There is a time interval between attainment of CW and cessation of growth, called the terminal growth period (TGP) (Figs. 1a and 2a). After the TGP, the larva begins to wander away from its food source to find a place to metamorphose. Ultimately, the final size of holometabolous insects is mostly determined by a combination of three factors: CW, TGP, and growth rate (GR) during the TGP (Shingleton et al., 2008). Moreover, the threshold size for metamorphosis or maturation, like CW in holometabolous insects, has been reported for crustaceans, amphibians, and fish, suggesting that such a phase transition in the growth schedule is a widely-occurring phenomenon in animal development (Day and Rowe, 2002). The physiological mechanisms of CW have been well studied in *Drosophila melanogaster* and *Manduca sexta*; for example, insulin pathways and/or oxygen levels have been shown to be involved in the sensing of critical weight (Callier et al., 2013; Callier and Nijhout, 2011; Koyama et al., 2014; Mirth et al., 2005). Interestingly, the combination of hormones required for commitment to metamorphosis is different between these species, and environmental sensitivity of the CW, such as the nutritional and temperature reaction norms, also differ (Davidowitz et al., 2003; Davidowitz and Nijhout, 2004; Ghosh et al., 2013; Layalle et al., 2008; Nijhout, 2015). These differences in physiology and reaction norms between species imply that the CW may have evolved through independent adaptations in each species. If

(a)

Pupation → Eclosion →

t_{TGP} t_P

| Larva | (TGP) | Pupa | Adult |

$t = 0$ t_{CW}^* t_{CG}^* t_{EC}

(b)

x
Environment

Feeding

E
Energy

b_L a b_I
Basal   Controllable   Basal

u^* $1 - u^*$

L I
Larval tissues   Imaginal tissues

(c)

I
Imaginal tissues

$L \xrightarrow{c}$
Larval tissues

A
Adult body

(d)

$t_{CG}^* \xrightarrow{g} A$
Developmental time   Adult body

μ_L m

ϕ
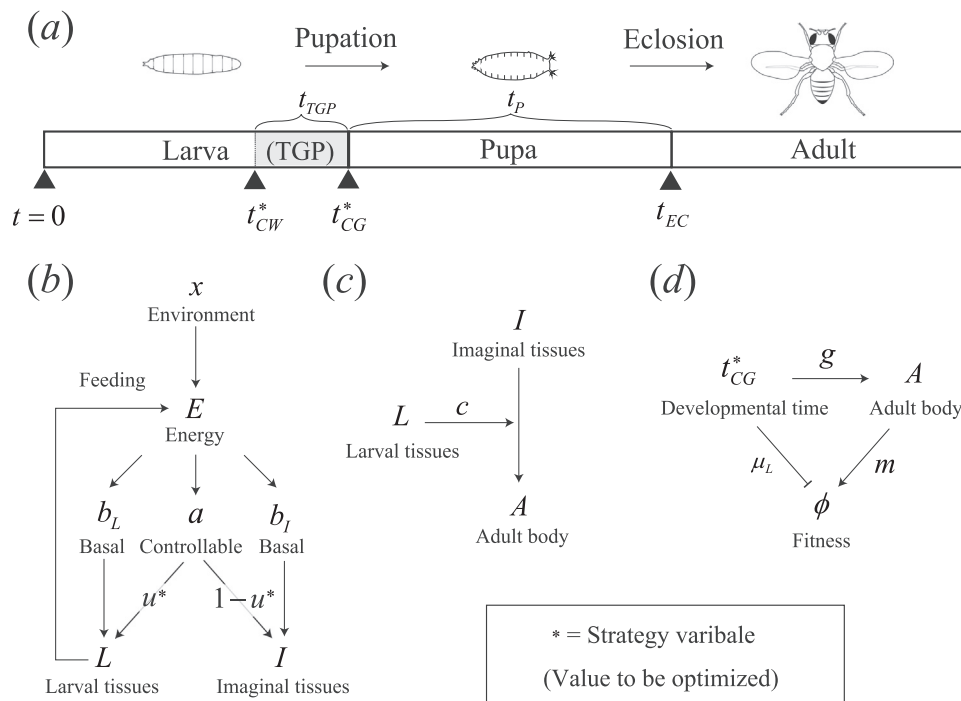Fitness

* = Strategy varibale
(Value to be optimized)

Fig. 1. Schematic representation of the life history model for holometabolous insects. (*a*) This life history model consists of larval, pupal, and adult stages. After hatching from the egg at time $t = 0$, the larva grows until the time of cessation of growth, $t = t_{CG}$, at which point the larva starts wandering to seek a place to pupate. Note that in a real situation, there exists a special time $t = t_{CW}$ at which larval weight reaches critical weight, which commits it to metamorphosis. The time interval between t_{CW} and t_{CG} is called the terminal growth period (TGP) or the interval to cessation of growth (ICG), the duration of which is denoted by $\Delta t_{TGP}: = t_{CG} - t_{CW}$. In our model, the critical weight and its timing t_{CW} are not explicitly assumed, and instead, as shown in the Results, they naturally appear as a consequence of optimal energy allocation. (*b*) A model for larval stage energy allocation to larval and imaginal tissues. During the larval stage, by feeding, the larva obtains energy E available for the allocation to growth of the larval and/or imaginal tissues, which is assumed to be a power function of L with an exponent k. The available energy E is divided into two portions: a controllable one aE and an uncontrollable one $(1 - a)E$. Of the controllable portion of energy aE, the proportion allocated to the larval (or imaginal) tissues is denoted by $au(t)$ (or $a(1 - u(t))$), where $u(t)$ is a control signal given as a function of time satisfying $0 \leq u(t) \leq 1$. Conversely, the uncontrollable portion $(1 - a)E$ consists of basal energy allocated to larval tissues $b_L E$ and to imaginal tissues $b_I E$ (i.e., $b_L + b_I + a = 1$). (*c*) The period from the time of growth cessation ($t = t_{CG}$) to that of eclosion ($t = t_{EC}$) is regarded as the pupal stage, and also includes the non-feeding wandering larval stage. Although the pupa does not feed, imaginal tissues can undergo growth and morphogenesis by using energy stored during the larval stage. (*d*) After eclosion, insects do not grow but are able to reproduce as long as they survive. The fitness of an individual insect φ increases with its size A_{EC} but decreases with developmental time t_{CG}. Since A_{EC} monotonically increases with t_{CG}, a trade-off exists: prolonging the developmental time improves the fecundity through further growth but inevitably reduces the survival probability until eclosion. Therefore, we can expect that optimal life history has a finite developmental time and size.

so, what is the adaptive significance of critical weight? This question is the focus of the present study.

To answer this, we developed a life history model for holometabolous insects and evaluated it from the perspective of energy allocation optimization (Roff, 2002; Stearns, 1992). The model consists of two variables: the size of the larval tissues and the size of the imaginal tissues. Imaginal tissues are precursors of prospective adult organs which are formed during embryonic or larval development. A common example is the 'wing imaginal disc', the primordium of the adult wing. With minimum assumptions on fitness functions, we show that the biphasic energy allocation to larval and imaginal tissues is optimal; almost all controllable energy is devoted to larval tissue until it reaches a certain threshold size, after which it is devoted to imaginal tissues until cessation of growth. Such biphasic growth of the imaginal tissues during larval development has been observed in many species of holometabolous insects (Chapman, 1998; Shingleton et al., 2008; Truman et al., 2006).

We would like to emphasize that, even without a priori assumptions about CW, its counterpart (i.e., the threshold) emerges as a natural consequence of optimal energy allocation. Using the proposed model, we can estimate the optimal timing for the attainment of CW from experimentally measurable quantities. For *Drosophila melanogaster* and *Manduca sexta*, the predictions are in good agreement with experimental observations, supporting the validity of our model. We then discuss the developmental plasticity of holometabolous insects in terms of optimal life history. Our model predicts that the relative value and timing of the CW should be constant and insensitive to environ-

mental change (i.e., scaling of growth scheduling), which provides a general interpretation of the phenotypic plasticity of the CW and TGP observed in *Drosophila melanogaster* and *Manduca sexta*. The scaling relationship allows the classification of the adaptive responses of CW and TGP into five possible types, most of which have been observed in living species. We also found that different types of plasticity can be caused by different fitness measures which should reflect ecological features of the focal insects, such as density-dependence or feeding specificity. Our theory and its consistency with experimental observations demonstrate the adaptive significance of critical weight.

2. Model

Our model for the life history of holometabolous insects includes three life stages: larva, pupa, and adult (Fig. 1a). As commonly assumed for insects, viability is given by an exponential function of time t, $l(t) = e^{-\mu t}$, at each stage; μ_L, μ_P and μ_A are the mortality in larvae, pupae, and adults, respectively (Roff, 1981).

2.1. Larval stage

At $t = 0$, a larva hatches from the egg and starts to feed and grow until the time of cessation of growth, $t = t_{CG}$, at which time the larva starts wandering to seek a place to pupate. The larval body consists of two different tissues: larval tissues and imaginal tissues. Imaginal tissues are precursors of prospective adult organs, and these weights (or sizes) are denoted by $L(t)$ and $I(t)$, respectively. At every moment of