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The trade-off between maturation and growth during accelerated development in frogs

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ABSTRACT

Developmental energetics are crucial to a species' life history and ecology but are poorly understood from a mechanistic perspective. Traditional energy and mass budgeting does not distinguish between costs of growth and maturation, making it difficult to account for accelerated development. We apply a metabolic theory that uniquely considers maturation costs (Dynamic Energy Budget theory, DEB) to interpret empirical data on the energetics of accelerated development in amphibians. We measured energy use until metamorphosis in two related frogs, *Crinia georgiana* and *Pseudophryne bibronii*. Mass and energy content of fresh ova were comparable between the species. However, development to metamorphosis was 1.7 times faster in *C. georgiana* while *P. bibronii* produced nine times the dry biomass at metamorphosis and had lower mass-specific oxygen requirements. DEB theory explained these patterns through differences in ontogenetic energy allocation to maturation. *P. bibronii* partitioned energy in the same (constant) way throughout development whereas *C. georgiana* increased the fraction of energy allocated to maturation over growth between hatching and the onset of feeding. DEB parameter estimation for additional, direct-developing taxa suggests that a change in energy allocation during development may result from a selective pressure to increase development rate, and not as a result of development mode.

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1. Introduction

How energy and matter are mobilized and allocated during development is a basic problem in developmental biology. It also has critical ecological implications by affecting the duration of the embryo stage and the environmental requirements (oxygen, temperature, water) for development (Seymour et al., 1991; Rombough, 1994; Marsh et al., 1999; Gillooly et al., 2002; Kamler, 2008). Most species develop as eggs but there is enormous interspecific variation in factors such as initial egg size and energy density, the cost of development, developmental rate and the developmental stage at hatching. Classic energy budgeting approaches partition energy use into maintenance, growth, reproduction and storage (Vleck et al., 1980; Hoyt, 1987; Vleck and Vleck, 1987; Vleck and Hoyt, 1991; Charnov et al., 2001; Gillooly et al., 2002) but do not explicitly consider the costs of 'maturation' such as tissue differentiation, nor its maintenance. Under such energy budget frameworks, it is therefore difficult to account for changes in the relationship between energy use, growth and differentiation, as occurs in accelerated development.

The energetics of amphibian development is strongly tied to developmental mode, which ranges from the ancestral state of entirely aquatic eggs and larvae, to terrestrial eggs with aquatic larvae, to direct development where fully-formed metamorphs emerge directly from eggs (Duellman and Trueb, 1986). The generally high oxygen availability in air allows for an increase in egg size in terrestrial breeders (Packard and Seymour, 1997) and, as a consequence, terrestrial and direct developers have the largest eggs (Salthe and Duellman, 1973). Interspecific studies indicate that larger egg size slows the rate of embryonic development (Bradford, 1984, 1990; Pauly and Pullin, 1988). However, one Australian Myobatrachid frog appears to be an exception to this rule. The aquatic breeding *Crinia georgiana* produces relatively large eggs that are comparable in size to those of the closely related terrestrial eggs of *Pseudophryne bibronii*. The two species also have similar adult size, produce loose egg clutches of similar egg number and breed under comparable temperatures (Seymour and Roberts, 1995). Despite these parallels in egg characteristics and reproductive traits, studies have shown that *C. georgiana* embryos develop almost two times faster than *P. bibronii* (Seymour and Roberts, 1995; Seymour, 1999).

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We therefore examine the development, growth and O_2 consumption of *C. georgiana* and *P. bibronii* under an identical incubation temperature until metamorphosis and compare the partitioning of energy using dynamic energy budget (DEB) theory (Kooijman, 2010).

DEB theory is a metabolic theory that is based upon mechanistic assumptions that are grounded within a number of stylized biological facts (Sousa et al., 2008; Kooijman, 2010; Lika et al., 2011; Nisbet et al., 2012). An organism's energy assimilation and utilization are described as functions of its state (age, size, etc.) and the state of the environment (temperature, food, etc.) (Nisbet et al., 2000). Developmental transitions, such as from embryo to juvenile (equivalent to amphibian larva), are linked to the level of maturity, a state variable of the model quantified as the cumulative energy used for development, E_H. The other two state variables are structure, which can be quantified as volume, length or mass, and reserve, quantified as energy content or mass.

In DEB theory all energy acquired by an organism follows a unidirectional flow, going first into reserve before it is allocated to different processes. The flow of energy can split but does not merge (Fig. 1). The main split in energy flow from reserve, called the κ-rule for allocation, indicates that a fixed fraction, κ, of mobilized reserve is used for somatic growth and maintenance and the remaining, $1-\kappa$, is used for maturity maintenance and maturation (in embryos and juveniles) or reproduction (in adults) (Kooijman, 2010). The concept of maturation as a destination of mobilized reserve energy makes very specific predictions for how variation in allocation of energy to maturity should affect respiration and growth, yet it is one of the least tested aspects of DEB theory. This distinction between growth and maturation allows us to not only examine energy used to reach a certain size, but also to reach a developmental stage (or level of maturity). We apply this theoretical framework to empirical data collected for *C. georgiana* and *P. bibronii* to understand the relationship between energy allocation to growth, maintenance and maturation and resultant developmental trajectories. Furthermore, DEB theory is applied to previously published data on two direct developers, *Crinia nimbus* and *Geocrinia vitellina*, to examine the influence of development mode on energy allocation.

2. Materials and methods

2.1. Egg collection and incubation

Embryos and juveniles were staged throughout experiments according to Gosner (1960). We refer to these developmental stages with respect to maturity level, E_H^i, where *i* represents Gosner stages 1 (oviposition)–46 (metamorphosis). Clutches of terrestrial *P. bibronii* eggs were collected from Watt's Gully Native Forest Reserve, 50 km from Adelaide, South Australia. Three clutches (E_H^{21}, approximately 22 days old) were collected in May 2008 and another clutch (E_H^{9}, approximately 3 days old) in June 2008. The clutches were taken to the laboratory, cleaned and raised until metamorphosis at 12 °C as described by Mueller and Seymour (2011). Field site temperature in the three weeks prior to collection of the older clutches averaged 12 °C (Australian Bureau of Meteorology, http://www.bom.gov.au), and therefore development rate was assumed to be similar to the clutches incubated in the laboratory from 3 days old at 12 °C.

One clutch of aquatic *C. georgiana* eggs (laid the previous night) was collected from the field, near Brookton Highway, 35 km southeast of Perth, Western Australia, in August 2008. Another four clutches (laid the previous night) were collected from captive adults held at the University of Western Australia in August 2009. Clutches were held at the University of Western Australia, transported by air to the University of Adelaide and raised until metamorphosis at 12 °C as described by Mueller and Seymour (2011). The incubation method was highly successful for both species, with approximately 90% survival to metamorphosis. Data for each clutch, which were of similar size within and between species and showed no significant differences in development, mass or respiration, were pooled.

2.2. Mass and energy density

Ova were dissected from fresh eggs, dried to constant mass over silica gel and weighed to 0.01 mg on an electronic balance (Mettler AE183, Greifensee, Switzerland). Embryos and juveniles were selected at random throughout development, killed by freezing and placed in Tyler's preservative (Tyler, 1962). They were dissected into body and yolk, dried over silica gel and weighed. Dried samples of fresh ova, hatchling gut-free body and yolk and metamorph gut-free body were homogenized using a mortar and pestle to make a pellet of at least 25 mg. The energy density of the pellets was measured with an 1107 semi-micro bomb of a 1261 bomb calorimeter (Parr, Moline, USA) after calibration with dry benzoic acid.

2.3. Oxygen consumption

O_2 consumption rates $\left(\dot{M}o_2\right)$ of embryos and juveniles were determined at 12 °C as described by Mueller and Seymour (2011). Briefly, $\dot{M}o_2$ until E_H^{35} (hindlimb toe maturation) were determined for individuals from the decrease in Po_2 within sealed water-filled respiratory chambers (0.67 mL, model 1271, Diamond General, Ann Arbor, MI,

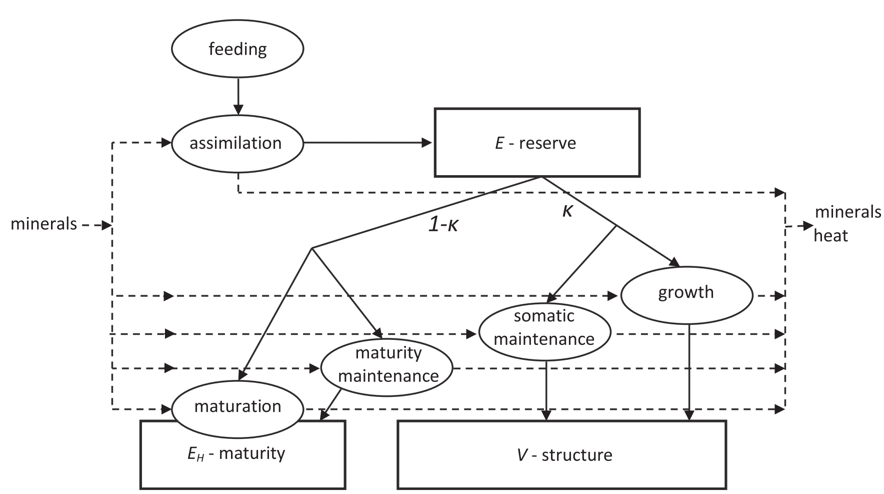

Fig. 1. Metabolism in a juvenile DEB organism. Rectangles represent state variables, ovals are processes, solid lines are flows from state variables to processes and vice versa and dashed lines are flows of minerals (O_2, CO_2, NH_3, H_2O) to and from processes. The processes of feeding and assimilation are absent in embryos.