



Effects of *Echinostoma trivolvis* metacercariae infection during development and metamorphosis of the wood frog (*Lithobates sylvaticus*)



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ABSTRACT

Many organisms face energetic trade-offs between defense against parasites and other host processes that may determine overall consequences of infection. These trade-offs may be particularly evident during unfavorable environmental conditions or energetically demanding life history stages. Amphibian metamorphosis, an ecologically important developmental period, is associated with drastic morphological and physiological changes and substantial energetic costs. Effects of the trematode parasite *Echinostoma trivolvis* have been documented during early amphibian development, but effects during later development and metamorphosis are largely unknown. Using a laboratory experiment, we examined the energetic costs of late development and metamorphosis coupled with *E. trivolvis* infection in wood frogs, *Lithobates [=Rana] sylvaticus*. *Echinostoma* infection intensity did not differ between tadpoles examined prior to and after completing metamorphosis, suggesting that metacercariae were retained through metamorphosis. Infection with *E. trivolvis* contributed to a slower growth rate and longer development period prior to the initiation of metamorphosis. In contrast, *E. trivolvis* infection did not affect energy expenditure during late development or metamorphosis. Possible explanations for these results include the presence of parasites not interfering with pronephros degradation during metamorphosis or the mesonephros compensating for any parasite damage. Overall, the energetic costs of metamorphosis for wood frogs were comparable to other species with similar life history traits, but differed from a species with a much shorter duration of metamorphic climax. Our findings contribute to understanding the possible role of energetic trade-offs between parasite defense and host processes by considering parasite infection with simultaneous energetic demands during a sensitive period of development.

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1. Introduction

Fundamental to understanding animal physiology is the concept of energetic trade-offs among the competing processes of growth, development, maintenance and reproduction (Stearns, 1989; Roff, 2001; Zera and Harshman, 2001; Lee, 2006). Among the multitude of physiological costs inherent to self-maintenance, immune defense against parasite infection is thought to be particularly costly (Martin et al., 2003; Lee, 2006; Hawley and Altizer, 2010). For example, basal metabolic rate of Collared Doves (*Streptopelia decaocto*) increased by a maximum of 8.5% in response to challenge by a novel antigen, corresponding with antibody production (Eraud et al., 2005). However, there are relatively

few studies quantifying the metabolic costs of immune challenge in wild vertebrate species, especially in response to parasites (Lochmiller and Deerenberg, 2000; Hawley et al., 2012). Costs of parasite defense are not limited solely to support of the immune system. They can also consist of repairing tissue damage, and can result from competition between the parasite and host for energy resources (Kristan and Hammond, 2000; Khokhlova et al., 2002; Sandland and Minchella, 2003).

Defense against parasites may elicit trade-offs with other functions or activities that require common resources, thereby influencing an animal's fitness (Lee, 2006; Hawley and Altizer, 2010). For example, wood frog tadpoles exposed to ranavirus showed elevated corticosterone, which was associated with a more rapid progression through metamorphosis at the expense of body weight and immune responses (Warne et al., 2011). This illustrates how intrinsic factors, such as particular developmental periods, require increased energy allocation. This can potentially limit the investment in other processes, such as immunity, and lead to increased fitness-related consequences of infection

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(Warne et al., 2011; Blaustein et al., 2012). Using this resource allocation framework helps explain why there may not be trade-offs between parasite defense and other demands unless they share required resources, occur simultaneously, or if available resources are insufficient to fuel competing demands (Lee, 2006; Hawley et al., 2012). Across a variety of host-parasite systems energetic costs of parasite infection were only evident or additive when there were competing energetic demands, such as during maximum activity, temperature stress, or during mammalian pregnancy or lactation (Lester, 1971; Meakins and Walkey, 1975; Hayworth et al., 1987; Munger and Karasov, 1989; Connors and Nickol, 1991; Booth et al., 1993; Chappell et al., 1996; Meagher and O'Connor, 2001; Kristan and Hammond, 2000, 2003; Hawley et al., 2012; Novikov et al., 2015). Therefore, it is important to investigate energetic costs of parasitism during periods of elevated energy demand to determine the overall impact of parasites on hosts (Robar et al., 2011; Warne et al., 2011).

Larval amphibians and trematode parasites have become a model system for investigating many aspects of host-parasite interactions and could be used specifically to test physiological trade-offs of parasite defense and development (Warne et al., 2011; Blaustein et al., 2012; Koprivnikar et al., 2012). *Echinostoma trivolvis* is a widespread digenetic trematode infecting larvae of several amphibian species as intermediate hosts and occasionally causing mortality and reduced growth, especially in very small larvae (Beaver, 1937; Fried et al., 1997; Schottoefer et al., 2003; Belden, 2006; Holland et al., 2007; Belden and Wojdak, 2011). Specifically, *E. trivolvis* metacercariae infect amphibian kidneys, causing renal inflammation, which can result in physiological dysfunction and edema (McClure, 1919; Faeh et al., 1998). Little is known about the immune response of larval amphibians to helminths, such as trematodes (Holland, 2009; Koprivnikar et al., 2012). However, *E. trivolvis* infection in amphibians is associated with granuloma formation, granulocyte infiltration, and a shift in the abundance and types of circulating leukocytes (Martin and Conn, 1990; Holland et al., 2007). Although some previous investigations of *E. trivolvis* infection in larval amphibians revealed reductions in growth with likely energetic underpinnings, no significant effects on host metabolic rate have been detected (Fried et al., 1997; Schottoefer et al., 2003; Orlofske et al., 2009, 2013). However, it is possible that effects to host metabolism may become evident during developmental periods that are more demanding, such as amphibian metamorphosis (Warne et al., 2011; Blaustein et al., 2012).

Studies of amphibian metamorphosis indicate that this is an energetically demanding period where total energetic costs and developmental costs are significant (*Hoplobatrachus* [= *Rana*] *tigerinus*, Pandian and Marian, 1985; *Anaxyrus* [= *Bufo*] *terrestris*, Beck and Congdon, 2003; and *Lithobates palustris*, Orlofske and Hopkins, 2009). Compensatory responses of hosts to parasites could be limited during metamorphosis because of reliance upon stored energy resources (Duellman and Trueb, 1986; Beck and Congdon, 2003) and the potential ecological vulnerabilities imposed by delayed metamorphosis (Wassersug and Sperry, 1977; Arnold and Wassersug, 1978; Downie et al., 2004).

Here, we examine the energetic costs of parasite infection concurrent with amphibian metamorphosis, as well as characterize the energetic costs of metamorphosis in wood frogs (*Lithobates sylvaticus*). We used a laboratory experiment to create a range of *E. trivolvis* metacercariae infection in amphibian hosts. We assessed the fate of metacercariae encysted within the pronephros or larval kidneys after completion of metamorphosis. While *Lithobates clamitans* tadpoles can eliminate echinostome metacercariae according to age-dependent process (Holland, 2009), it is unknown whether metacercariae are shed during, or interfere with, the restructuring of the amphibian kidneys during metamorphosis. We predicted high survival given our realistic, gradual exposure procedure (as in Orlofske et al., 2013), but reduced growth and longer development time associated with infection intensity due to increased metabolic costs of infection. We predicted elevated total and developmental energy costs, longer period of metamorphic climax, and smaller size after completing metamorphosis accompanying

E. trivolvis infection. Finally, we investigated the role of duration of metamorphic climax and body size on the developmental costs and total costs of amphibian metamorphosis.

2. Materials and methods

2.1. Study system

Echinostoma trivolvis is a model parasite used frequently to investigate host-parasite interactions (Thiemann and Wassersug, 2000a,b; Belden, 2006; Koprivnikar et al., 2006; Toledo et al., 2007; Griggs and Belden, 2008; Johnson and McKenzie, 2008). *Echinostoma trivolvis* requires three hosts to complete its life cycle. The first intermediate host is the ubiquitous snail *Planorbella trivolvis* which is infected by free swimming miracidia that hatch from eggs deposited in definitive host feces (Schmidt and Fried, 1997). A wide array of second intermediate hosts can be infected by the second free-living stage (cercariae), including snails, and larvae and adults of several amphibian species (Huffman and Fried, 1990; Kanev et al., 1995). The definitive hosts include a variety of birds and mammals, particularly muskrats, which consume the infected second intermediate hosts (Johnson and McKenzie, 2008; Detwiler et al., 2012).

Wood frogs (*Lithobates* [= *Rana*] *sylvaticus*) are the most broadly distributed amphibian in North America (Redmer and Trauth, 2005) and are host to a diversity of adult and larval parasites (McAllister et al., 1995). One of the most commonly documented trematodes of wild *L. sylvaticus* tadpoles is *Echinostoma trivolvis* (Najarian, 1955; McAllister et al., 1995; Woodhams et al., 2000). In *L. sylvaticus*, natural infections with echinostomes averaged 90 metacercariae per host (Woodhams et al., 2000).

2.2. Parasite culture

Methods for obtaining infected snails follow Orlofske et al. (2013). Briefly, *Echinostoma trivolvis* eggs were collected by mixing feces from laboratory-infected golden hamsters (*Mesocricetus auratus*) with a small amount of water, and adding it to containers with laboratory-raised *Planorbella trivolvis* snails. We did not quantify the number of eggs in the feces dilution, but similar collections from the same hamsters yielded 666–1043 eggs/mL. Water in the snail containers was left undisturbed for 3 weeks to allow for hatching of *E. trivolvis* eggs (Belden et al., 2009). We maintained snails for 3 weeks at room temperature with lettuce and flake fish food provided ad lib and 50% water changes performed weekly. We screened snails for infection by placing them in individual containers warmed with an incandescent bulb and microscopically examined the water for cercariae (Schmidt and Fried, 1996). After we confirmed parasite infection, we maintained snails individually at 8–10 °C to prevent mortality resulting from reinfection (Kuris and Warren, 1980). This entire procedure took place in September 2007 and again in February 2008, resulting in a total of 27 infected snails.

2.3. Amphibian collection and maintenance

On February 22, 2008, we collected four freshly laid *L. sylvaticus* egg masses from an ephemeral pond in Montgomery County, Virginia. We transferred egg masses gradually from pond water to a 3:1 mix of dechloraminated (ChlorAm-X®, AquaScience Research Group, Inc., North Kansas City, MO, USA) tap water (53.7 mg/L CaCO₃) and well water (364 mg/L), to create a mixture with an acceptable hardness level of 108 mg/L of CaCO₃. We removed sixty healthy *L. sylvaticus* eggs with intact jelly coats from each egg mass (240 total eggs) and acclimated them together in a single bin containing 6 L of water. We maintained the eggs at 18 °C using a temperature-controlled environmental chamber (Adaptis, Conviron, Manitoba, Canada). All eggs hatched on March 2, and 80 tadpoles were selected randomly for the experiment

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