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Original Article

Maternally chosen nest sites positively affect multiple components of offspring fitness in a lizard

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Maternal nest-site choice is a behavioral phenotype with transgenerational consequences that can appear at multiple stages of offspring ontogeny. In many reptiles, the microenvironment surrounding eggs (e.g., moisture) can affect multiple aspects of offspring fitness across several life stages (e.g., embryo survival, phenotypic development, and posthatching survival). Thus, natural selection should favor maternal nesting behaviors that positively affect both embryonic and postembryonic ontogenetic trajectories. We tested this hypothesis in a 2-part laboratory experiment using the brown anole lizard (*Anolis sagrei*). In the first experiment, gravid lizards were given a choice of nesting substrates containing 5 levels of moisture content. By incubating eggs at the same 5 moisture levels, our second experiment tested if maternal choice of nest substrate facilitates embryonic development and enhances offspring quality and viability. Females strongly preferred nesting substrates with high moisture content, and these conditions yielded high hatching success, large offspring size, and overall increased offspring survival. These results suggest that selection has adaptively matched maternal nesting behaviors, embryonic development, and posthatching phenotypes in ways that enhance both offspring and parental fitness. In addition, our results highlight the importance of incorporating multiple life-history stages when assessing the fitness consequences of transgenerational effects. *Key words: Anolis sagrei, brown anole, incubation moisture, maternal effects, nest-site choice, ontogenetic trajectory, phenotypic plasticity. [Behav Ecol]*

INTRODUCTION

Evolutionary theory predicts that differential selection will favor phenotypes that enhance fitness (Darwin 1859). Although this prediction suggests that phenotypes of high fitness will occur in relatively high frequencies, the persistence of low-fitness phenotypes is still observed within populations. This persistence of less-fit phenotypes can be explained by multiple factors (e.g., constraints, plasticity, unstable environments, and mendelian inheritance) and serves as an important source of phenotypic variation on which natural selection operates (Falconer and Mackay 1996; West-Eberhard 2003). One explanation for why seemingly deleterious phenotypes persist involves variation in the timing of when fitness returns to a given phenotype are actually manifested. For example, the fitness return of a transgenerational parental effect can occur at multiple life-history stages and at different times during offspring ontogeny. Thus, an effect that has a seemingly negative impact on parental fitness may actually enhance fitness at some later point in life (Plaistow et al. 2007; Marshall 2008). These types of delayed benefits present a challenge for studies of the adaptive significance of parental effects (Marshall and Uller 2007).

The behavioral choice of oviposition site provides an excellent example of a maternal effect whose fitness consequences may be realized at 1 or more stages of offspring ontogeny. In many oviparous organisms, the developmental environment chosen by mothers has major consequences on both embryonic and postembryonic ontogenetic trajectories (Fox et al. 1997). For example, environmental conditions of a nest site not only impact embryo survival but also the developmental trajectory of fitness-relevant phenotypes and growth in ways that can influence posthatching survival and reproductive success (Hunter et al. 2001; Jensen et al. 2009). Additionally, in some cases, conditions that maximize 1 phenotypic attribute of the offspring may not always be optimal for other phenotypes (Shine and Harlow 1996; DuRant et al. 2010). This conflict poses a major challenge to nesting females because they need to balance between sites that might optimize different aspects of their offspring's phenotype. Ideally, selection should optimize maternal nest-site choice behaviors so that parental and offspring fitness are enhanced across multiple stages of embryonic and postembryonic ontogeny (Refsnider and Janzen 2010). Thus, researchers must identify long-term effects of different developmental environments to gain insights into the adaptive value of this critical maternal effect.

Oviparous reptiles make excellent models for examining how maternal nest-site choice can impact multiple aspects of offspring fitness during embryonic and postembryonic stages. Because reptilian eggs and embryos are highly sensitive to environmental conditions and most species do not exhibit postoviposition parental care, researchers can directly evaluate the impact of maternally chosen nest conditions on ontogenetic trajectories. In nearly all species examined, thermal and hydric conditions affect hatchling phenotypes in ways that can impact fitness (Elphick and Shine 1998; Brown and Shine 2004). Moisture and temperature both significantly affect embryo development and hatching success in reptiles (Madsen and Shine 1999; Hokit and Branch 2004;

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