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Do female newts modify thermoregulatory behavior to manipulate egg size?

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ABSTRACT

Reproductive females manipulate offspring phenotypes by modifying conditions during embryogenesis. In ectotherms, the environmental control over embryogenesis is often realized by changes in maternal thermoregulation during gravidity. To determine if reproduction influences thermoregulatory behavior in species where females lay eggs shortly after fertilization (strict oviparity), we compared preferred body temperatures (T_p) between reproductive (egg-laying) and non-reproductive female newts, *Ichthyosaura alpestris*. Next, we exposed reproductive females to temperatures mimicking T_p ranges of reproductive and non-reproductive individuals to find out whether the maternally modified thermal regime influences ovum and jelly coat volume, and early cleavage rates at the time of oviposition. In the thermal gradient, reproductive females maintained their body temperatures within a narrower range than non-reproductive individuals. The exposure of ovipositing females to temperatures preferred during their reproductive and non-reproductive period had a negligible influence on egg size and early cleavage rates. We conclude that the modification of maternal thermoregulatory behavior provides a limited opportunity to manipulate egg traits in newts.

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1. Introduction

Mothers affect their offsprings' phenotype not only via genes but also with environmental conditions during embryonic development (maternal effect). Countless studies have demonstrated that maternally-manipulated environments benefit developing embryos (Lorioux et al., 2013; Madsen and Shine, 1999; Rieger et al., 2004). On the other hand, females can also behave in the opposite way, i.e. by providing detrimental conditions for individual offspring (Gripenberg et al., 2007; Rosenheim et al., 2008; Scheirs et al., 2000). Current conceptual advances in maternal effect studies resolved this paradox by viewing the adaptive maternal effect from the female rather than offspring's lifetime reproductive success (Marshall and Uller, 2007). From this view, maternally-provided conditions may be beneficial, neutral, or even detrimental to developing embryos. Despite the conceptual progress in this field, benefits of some maternal behaviors remain unclear.

In many ectotherm taxa, gravid females often modify the mean or variance in body temperatures that benefit her offspring (Shine and Downes, 1999; Mathies and Andrews, 1997; Rodríguez-Díaz

and Braña, 2011). Originally, the thermoregulatory shift was explained as a solution to the conflict between disparate thermal optima for mother and offspring phenotypes (Beuchat and Ellner, 1987). In agreement with the current view (see above), it has been recently proposed that maternal thermoregulation may favor not only offspring survival, the maternal manipulation hypothesis (Shine, 1995), but also female performance (Schwarzkopf and Andrews, 2012). However, because females of most examined taxa, squamate reptiles, deposit their eggs in later developmental stages (stages 30–40 after Dufaure and Hubert, 1961), determining whether maternal thermoregulatory behavior primarily increases female performance or offspring survival seems a challenging task. One previously omitted solution to the 'chicken and egg' problem is the focus on maternal thermoregulation in non-squamate taxa with the most primitive reproductive mode, when a female oviposits shortly before or after fertilization (strict oviparity). If strictly oviparous females modify their thermoregulatory behavior during reproduction, it clearly shows that maternal thermoregulatory adjustments evolved primarily for other reasons than the manipulation of offspring phenotypes.

Among the few studies on non-squamate systems examining the influence of reproduction on preferred body temperatures (T_p ; Gvoždík, 2005; Webber et al., 2015), tailed amphibians, newts, seem particularly suitable for this task. Reproductive females of the Italian crested newt, *Triturus cristatus*, modified both their T_p

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mean and range relative to their non-reproductive counterparts (Gvoždík, 2005). Newts are strictly oviparous species and their eggs are laid before or shortly after the first cleavage (Griffiths and de Wijer, 1994). Accordingly, fertilized eggs stay in the oviduct for 4.5–12 h depending on temperature (Epperlein and Junginger, 1982; Bonacci et al., 2005). In contrast, newt embryonic development lasts about 15 days under thermally fluctuating conditions (Měráková and Gvoždík, 2009), and thus maternal thermoregulatory behavior provides a negligible opportunity for maternal thermal manipulation of offspring phenotypes during embryonic development. However, female body temperatures affect ovum size (Kaplan, 1987), and thereby offspring fitness-related traits, in amphibians (Bernardo, 1996; Kaplan, 1980; Semlitsch and Gibbons, 1990). Hence, newt maternal thermoregulation may affect offspring phenotypes in this previously unexplored way. In addition, because temperature influences most functions and processes within an organism (Cossins and Bowler, 1987), it may also modify the production of egg jelly coats. The jelly coating has many functions ranging from fertilization to protection (Shu et al., 2015), and thus their volume surrounding the oocyte is potentially adaptive. Whether maternally-modified temperatures affect newt ovum or jelly coat size is unknown.

In this study, we examined if reproductive alpine newt females, *Ichthyosaura alpestris*, modify egg size and early cleavage rates by modifying their thermoregulatory behavior. We expect that in strictly oviparous ectotherms, i.e. not carrying embryos in their bodies, the only possibility to effectively manipulate offspring phenotypes through maternal thermoregulatory behavior is via its effect on egg traits. Our aim was twofold. First, we tested the influence of reproductive state on T_p in female newts. Second, we exposed reproductive female newts to temperatures mimicking T_p ranges of reproductive and non-reproductive females to determine whether various thermal regimes affect the size and early cleavage rate of their eggs.

2. Materials and methods

2.1. Study species and maintenance

Ichthyosaura alpestris is a medium-sized (total length=90–120 mm) newt that is widely distributed across most of continental Europe. The aquatic reproductive period lasts from April till June. Females oviposit 200–300 eggs during this period. Eggs are laid individually and wrapped in aquatic vegetation, providing eggs with protection against predators (Orizaola and Braña, 2003) and UV-radiation (Marco et al., 2001). This species shows distinct thermoregulatory behavior both in the laboratory and in semi-natural conditions (Balogová and Gvoždík, 2015; Marek and Gvoždík, 2012). Female oviposition preferences are also guided by water temperature (Dvořák and Gvoždík, 2009; Kurdíková et al., 2011), which affects offspring performance and life-history traits (Kurdíková et al., 2011; Měráková and Gvoždík, 2009).

We captured adult newts (snout-vent length [SVL]=45–55 mm) by hand from a population near Jihlava, Czech Republic. In April 2009, we used 25 pairs (1:1 sex ratio) for testing the influence of reproduction on female preferred body temperatures. In April 2011, we took another 26 pairs for testing the effect of temperature on egg size. Newts (one male and one female) were placed in aquaria (50 × 30 × 18 cm high) filled with non-chlorinated well water. Each aquarium was equipped with clumps of aquatic plants (*Egeria densa*) to provide egg laying substrate and shelter, and a piece of Styrofoam to allow newts to leave the water. Aquaria were placed in a room with light and thermally fluctuating (12–22 °C) regimes mimicking conditions in their natural habitat (Dvořák and Gvoždík, 2010). In November 2009, newts were

reshuffled to keep both sexes separate and aquaria were transferred to a walk-in climatic chamber for wintering at 4 °C until the end of March 2010. Newts were fed with live food, *Tubifex* worms, earthworms (*Eisenia* sp.), and chironomid larvae, once or twice per week. Water was changed on a weekly basis.

2.2. Preferred body temperatures

To test the influence of reproduction on T_p , we paired randomly chosen females ($n=11$) with males in the beginning of April 2010. After a few days, the females started egg-laying, and thus they were denoted as reproductive. The unmated females ($n=14$) represented the non-reproductive group.

Preferred body temperatures were measured in a stainless steel tank (240 × 60 × 60 cm high). The tank was divided into three longitudinal lanes. Each lane was partially separated into 12 partitions. The tank was filled with water to 4 cm. A computer controlled series of Peltier modules and a heat recuperation system maintained a horizontal thermal gradient (5–32.5 °C) in steps of 2.5 °C per partition. Each partition contained a clump of Java moss, *V. dubyana*, (3 g of wet mass) to provide reproductive females with laying substrate equally across temperatures. Water was kept at oxygen-saturated levels using an aeration stone in each partition. The tank was located in a room with stable temperature conditions (18 ± 2 °C). Lighting was provided by fluorescent bulbs (300 lx on water surface) during the day (6:00–18:00) and two red bulbs (< 5 lx) allowed the recording of newt behavior during the night.

Because feeding and digestion influence T_p in newts (Gvoždík, 2003), and newts generally have food in their stomachs (Griffiths and Mylotte, 1987), newts were fed 24 h before the beginning of T_p trials. Three randomly selected females were placed into the tank (17.5 °C) 12 h before the beginning of a trial (20:00) for habituation to tank conditions. Female behavior was continuously (12 fps) recorded using a digital surveillance system (V-Guard RT4, Chateau Tech. Corp., Taiwan) for the following 24 h (8:00–20:00). After a trial, egg numbers and oviposition temperatures were recorded for each female. Oviposition temperatures were characterized by their mean and range (max–min) for each female. Later, we analyzed video files to obtain information about newt body temperatures by interpolating horizontal positions, the partition number, with known water temperatures. Because body temperatures of small to medium sized aquatic ectotherms closely match surrounding water temperature (Lutterschmidt and Hutchison, 1997), we considered this indirect method as a reliable, non-invasive, and non-disturbing approach to obtain body temperatures in this system. We recorded newt positions at 10 min intervals, which yielded 144 temperatures from each individual. From an individual T_p distribution, we calculated mean, and boundaries of the T_p range as 10th and 90th percentiles. Previous studies (Hadamová and Gvoždík, 2011; Gvoždík, 2015) proved that this method is sufficient to eliminate possible outliers from individual T_p distribution in newts. Motor activity index was estimated as the number of crosses between partitions during a trial.

2.3. Egg oviposition

Reproductive females captured in 2011 were individually placed in aquaria (41 × 23 × 17 cm high) filled with 3 L of water and equipped with a thermostatic 50 W heater (Eheim/Jäger, Wüstenrot, Germany) and a clump of aquatic vegetation to provide substrate for oviposition. Females were randomly distributed between two groups that were exposed to temperatures matching the T_p range of reproductive and non-reproductive females (Fig. 1). Aquaria of each group were placed in a separate climatic room. The required thermal regime was achieved by heating water to

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