



New insights into parental effects and toxicity: Mate availability and diet in the parental environment affect offspring responses to contaminants



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ARTICLE INFO

Article history:

Received 17 January 2013

Received in revised form

22 April 2013

Accepted 1 May 2013

Keywords:

Biomphalaria glabrata

Diet

Metal

Inbreeding

Transgenerational effect

ABSTRACT

Parental effects manifest as alterations in offspring phenotype resulting from the parental phenotype and/or parental environment. We evaluated the effects of parental diet quality and mating strategy on the toxicant tolerance of offspring in *Biomphalaria glabrata* snails. We raised snails either individually (self-fertilizing) or in groups of three (outcrossing) on a diet of uncooked lettuce, fish food, cooked lettuce, or cooked lettuce plus fish food. We then exposed their offspring to cadmium and malathion challenges. Cadmium tolerance varied with parental diet and was greater in the offspring of outcrossing snails than self-fertilizing snails. Malathion tolerance was not affected by parental diet but was greater in the offspring of outcrossing snails. These results indicate that offspring responses to stressors are heavily influenced by parental experience, but may depend on the specific stressor and the mechanism of action and/or detoxification.

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1. Introduction

Parental effects are influences on offspring phenotype that result from the parental phenotype or environment (Bernardo, 1996; Mousseau and Fox, 1998; Badyaev and Uller, 2009). Parental effects act on offspring not via inherited DNA sequences, but by other means including epigenetic effects, parental care, parental modification of the offspring environment, and transfer of nutrients and hormones to offspring (see Badyaev and Uller, 2009 and references). Many ecological studies have shown that biotic and abiotic factors in the parental environment can be important determinants of offspring development and fitness. For example, exposure of female insects to environmental cues such as short photoperiods, cool temperatures, few potential hosts, or high conspecific densities can increase the proportion of diapausing or dispersive offspring (Mousseau and Fox, 1998). In snails, exposure to predator threat increases time to first reproduction, decreases reproductive output, and alters offspring stressor tolerance (Plautz et al., 2013). And in many reptiles, the temperature of the location where a female lays her eggs determines the sex ratio of her

offspring (Shine, 1999). Though some parental effects have short-term effects on offspring, the effect of others is lifelong.

The maternal environment also influences her nutritional status, which can in turn affect her offspring. In a wide variety of animals, including insects, amphibians, and birds, maternal body condition influences the number of eggs produced, egg size, and nutrient and hormone composition of eggs (Rossiter, 1996; Mousseau and Fox, 1998). The nutrients and hormones transferred from mother to offspring have a strong influence on offspring size and development that can translate into lifelong effects on growth and survival rates (Bridges and Heppell, 1996; Chambers and Leggett, 1996). As an illustration, female Belding's ground squirrels (*Spermophilus beldingi*) given supplemental food produced young that were 28% heavier when they emerged from their natal burrows than the offspring of non-supplemented adults (Trombulak, 1991). In the offspring of moths (*Plodia interpunctella*) fed either a poor or good quality diet, immune reactivity as measured by hemocyte count and phenoloxidase activity was reduced compared to controls when only one parent was fed the poor quality diet and lowest when both parents were fed the poor quality diet (Triggs and Knell, 2012). Additionally, when juvenile fruit flies (*Drosophila melanogaster*) were fed poor quality food, the offspring of parents raised on poor quality food as larvae had decreased time to pupation compared to the offspring of parents fed good quality food (Vijendravarma et al., 2010). Parental nutrition can also influence offspring toxicant

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tolerance, as in the case of *Daphnia magna* cultures with low food availability producing offspring with greater tolerance to cadmium (Enserink et al., 1990) and the insecticide fenvalerate (Pieters and Liess, 2006) than the offspring of cultures with high food availability. Overall, available evidence indicates that maternal nutritional status can be an extremely important factor in production and development of offspring. However, while the detrimental effects of maternal food limitation on offspring are well-recognized, few studies have evaluated the effects of parental diet quality.

Another factor that can significantly affect offspring fitness is the parental reproductive strategy. Self-fertilization a common reproductive strategy, particularly in some invertebrates, but also represents a type of inbreeding, which can lead to the loss of heterozygosity and eventually to inbreeding depression (Brown et al., 2009). Studies on birds and mammals that are obligate outcrossers have shown that inbreeding leads to reductions in birth weight, survival, reproduction, and resistance to disease, predation and environmental stressors (Kellera and Waller, 2002). Specifically, an insular population of inbred song sparrows (*Melospiza melodia*) displayed reduced hatching success and juvenile survival rates (Keller, 1998) and inbred birds experienced a higher mortality rate than other birds during a severe storm (Keller et al., 1994). Also among these sparrows, environmental stress interacted with inbreeding such that the nests of inbred females had a greater reduction in hatching success during rainy periods than the nests of non-inbred females (Marr et al., 2006). Fewer data, however, are available for species that have a mixed mating strategy that includes both outcrossing and self-fertilization as generally viable modes of reproduction. In one example, *Bulinus globosus* snails produced by either self-fertilization or outcrossing displayed several differences in life history traits in first generation offspring. Outcrossed snails had a shorter time to hatch, higher survival at hatching, and produced more eggs than selfed snails. Selfed snails were larger than outcrossed snails 15 days after hatching, but smaller at 60 and 90 days post-hatch (Jarne et al., 1991). While inbreeding can lead to a variety of detrimental effects on organism fitness, particularly in combination with environmental stressors, few studies have addressed potential inbreeding effects in animals with a mixed mating strategy.

Data thus far has shown that parental nutrition and mating strategy can have significant effects on offspring development, but relatively little is known about the effects of these factors on offspring tolerance to chemical contaminants. Both diet and the presence (or absence) of mating partners are likely to vary in natural environments and therefore have implications for how populations respond to environmental stressors, including chemical contaminants. To better understand the effect of parental nutritional environment and mating strategy on offspring traits, we raised *Biomphalaria glabrata* snails on one of four diets and housed them either alone or with same-age conspecifics in a factorial design. *B. glabrata* are freshwater gastropods that are self-fertilizing hermaphrodites but preferential outcrossers and have been used previously as model organisms to study ecological and evolutionary responses to environmental stress (e.g., Salice et al., 2010). We then recorded survival of their offspring in cadmium and malathion challenges. We hypothesized that offspring toxicant tolerance would be lower in snails produced by self-fertilization compared to outcrossing and also that tolerance would higher in offspring produced by parents that were reared on diets that enhanced parental growth and reproduction.

2. Material and methods

2.1. Parental snail study design

B. glabrata (M-line and BS90 strains) were acquired from the Biomedical Research Institute in Rockville, MD and cultured in the laboratory for >3 yrs (>9

generations) at The Institute of Environmental and Human Health at Texas Tech University in Lubbock, Texas. We combined the two strains to increase overall genetic diversity. Culture tanks held >30 adult snails apiece, with at least five tanks maintained at all times to minimize isolation and potential inbreeding. *B. glabrata* is a freshwater pulmonate snail and a hermaphrodite which can self-fertilize when isolated but will preferentially outcross when housed with conspecifics (Mavarez et al., 2002). Adult snails from culture tanks were placed in three, 2 L BPA-free plastic tubs of reconstituted lab water (3.0 g CaSO₄, 3.0 g MgSO₄, 0.2 g KCl, and 4.9 g NaHCO₃ to 50 L deionized water) with 3 adults of each strain per tub to produce mixed-strain offspring. Snails were then placed in a 25 °C incubator with a 12:12 light:dark cycle and fed cooked romaine lettuce *ad libitum*. After ≥1 month, egg masses were collected from these tubs for experimental use.

Snails were housed in glass jars filled with lab water in a 25 °C incubator with a 12:12 light:dark cycle and water volume was increased from 50 to 100 mL per snail as snails grew. Water was changed twice per week and snails were fed *ad libitum*. Snails were raised from 6 days to 12 weeks old on a diet of uncooked romaine lettuce (UL), cooked romaine lettuce (CL), fish food (FF; crude protein minimum 44%, crude fat minimum 10%, fatty acids 3%; Nutrafin Max Spirulina Flakes, Rolf C. Hagen Corp., Massachusetts, USA), or cooked romaine lettuce plus fish food (CL + FF) with 20 jars per diet. Diets selected represent a subset of commonly used diets for laboratory studies with freshwater gastropods. Within each diet treatment, 10 jars contained three snails each and 10 jars contained only one snail. Since *B. glabrata* prefers to outcross (Mavarez et al., 2002), this was designed to evaluate the effects of mating strategy (self-fertilizing or outcrossing) on offspring stressor tolerance.

We used parental body condition as an indicator of diet quality, with the assumption that higher quality diets would be positively associated with higher parental survival, reproductive output, and size. To measure parental body condition on each diet, we recorded survival, snail shell length, and reproductive parameters. Snail shell length was measured using calipers to 0.01 cm when snails were 36 and 68 days old and egg mass time to hatch and hatching success were measured at the end of the study (snails 11 weeks old). At each water change, egg masses were counted and removed from jars and a subsample of 4 egg masses per jar was taken on days 29 (start of reproduction)–57 to quantify the number of eggs per egg mass.

2.2. Offspring toxicant exposures

To evaluate the effect of parental diet and mating strategy on developmental tolerance to chemical stressors, we collected egg masses when snails were 11 weeks old and exposed one ≤24 h old egg mass per parental replicate each to 25 µg/L cadmium and 8 mg/L malathion and recorded time to hatch and hatching success. These test concentrations of cadmium and malathion were based on pilot study concentrations which decreased but did not eliminate egg mass hatching success. All cadmium exposure containers were soaked in 25 µg/L cadmium for 24 h before experimental use.

For contaminant survival challenges of juvenile offspring, one egg mass per parental jar was collected for each contaminant when experimental parental snails were ≥9 weeks old and placed in clean lab water to hatch. Hatchlings were fed fish food immediately after hatching, but were not fed during contaminant survival challenges. When juvenile offspring were ≤48 h old, four snails per egg mass were randomly selected and placed in 100 mL of lab water. For the malathion survival challenge, juvenile offspring were housed in 125 mL glass jars in 100 mL lab water and exposed to 12.5 mg/L malathion. Mortality and snail location in jars (below, at, or above water line) were recorded at 3, 24, and 48 h post-exposure. Snail location was noted because *B. glabrata* can react to a stressor by moving up to the water line or above it, potentially altering their exposure (S.C. Plautz, unpublished data). For the cadmium survival challenge, snails were housed in 125 mL BPA-free plastic containers and exposed to 300 µg/L cadmium in 100 mL lab water. A higher cadmium concentration was used for the juvenile challenge because cadmium tolerance increases from developmental to juvenile and adult stages (Salice and Roesijadi, 2002). Mortality was recorded every 12 h for 120 h. All cadmium exposure containers were soaked in 300 µg/L cadmium for 24 h before experimental use. Ten parental trios were randomly selected for juvenile survival controls. For these controls, four juvenile snails from each parental trio were placed in a 125 mL container (5 glass and 5 plastic) with 100 mL lab water and mortality was recorded every 12 h for 120 h. Different durations were used for malathion and cadmium survival challenges because of differences in the responses of snails to these chemicals. When snails were exposed to cadmium, mortality occurred gradually, while exposure to malathion caused either no mortality at low concentrations or a rapid die-off at higher concentrations followed by little additional mortality.

2.3. Chemicals

Cadmium is typically found in freshwaters at concentrations <1 µg/L, but can reach 10 µg/L in areas of environmental disturbance (World Bank Group, 1999) and has been measured at >40 µg/L at contaminated sites (Environmental Integrity Project and Earthjustice, 2010). Malathion concentrations in freshwater are also usually <1 µg/L (Starnier et al., 2005; Klecka et al., 2010), but can reach 30 µg/L immediately following malathion application to surrounding areas (Keller and Ruessler, 1997). Both cadmium and malathion were used as model chemical

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