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Maternal food availability affects offspring performance and survival in a viviparous lizard

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Summary

1. Whether maternal effects are adaptive or not has been a long-standing topic of discussion in evolutionary ecology. The effects of maternal diet on offspring have been addressed by several studies on diverse organisms, but results are typically conflicting or inconclusive.

2. In this study, we conducted food manipulation experiments with a factorial design (high and low maternal food conditions × high and low offspring food conditions) in a viviparous lacertid lizard (*Eremias multiocellata*) to test four competing hypotheses on the evolutionary significance of maternal effects: environmental matching hypothesis, low-food compensation hypothesis, low-food pathology hypothesis and no-compensation hypothesis.

3. We found that offspring under the maternal low-food treatment had higher growth and survival rates than those under the maternal high-food treatment, supporting the low-food compensation hypothesis rather than the environmental matching hypothesis, which has been widely accepted as an explanation for the adaptive significance of maternal effects.

4. Our study highlights the importance of testing multiple competing hypotheses that involve both adaptive and non-adaptive explanations when studying the evolutionary significance of phenotypic plasticity.

Key-words: adaptive plasticity, *Eremias multiocellata*, food availability, growth, hatchling, maternal effect, reptile, survivorship

Introduction

The importance of maternal effects, as a phenomenon that allows the passing of environmental information through generations by plasticity rather than by direct genetic modifications, has gained increasing scientific attention since the 20th century (Scheiner 1992; Bernardo 1996a; Mousseau & Fox 1998b; Uller 2008). Many studies have demonstrated that maternal environment and experience can profoundly affect the morphological, behavioural and physiological traits of offspring (Einum & Fleming 1999; LaMontagne & McCauley 2001; Galloway 2005; Du 2006; Marshall 2008; Wolf & Wade 2009; Johnson *et al.* 2014; Stahlschmidt & Adamo 2015; Warner *et al.* 2015; Schwanz 2016), and may in turn influence adaptation of populations to rapidly changing environments prior to evolution via genetic adaptation (Reed, Schindler & Waples 2011; Parker *et al.* 2012). Therefore, maternal effects are critical for understanding the interplay between evolution and ecology in determining the species response to environmental change.

Whether maternal effects are adaptive has been a long-standing topic of discussion (Mousseau & Fox 1998a; Galloway & Etterson 2007; Marshall & Uller 2007). Although various studies attempt to identify the adaptive significance of maternal effects in diverse organisms, from plants to invertebrates to vertebrates (Galloway 2005; Steiger *et al.* 2007; Donelson, Mccormick & Munday 2008; Itonaga, Jones & Wapstra 2012; Araminaite *et al.* 2014; Henderson *et al.* 2014), it remains controversial whether maternal effects among species are adaptive or not. Some studies have indicated that mothers can adjust the phenotype of their offspring to match the changes in the local environment (Mousseau & Dingle 1991; Agrawal, Laforsch & Tollrian 1999). For example mothers inhabiting a stressful environment produce offspring better suited to that stress compared to mothers that are not exposed to stressful conditions (Mousseau & Fox 1998a; LaMontagne & McCauley 2001; Buechler *et al.* 2002). However, in other cases, maternal effects are non-adaptive or even have a negative influence on their offspring fitness as a result of physiological side effects (Heath & Blouw 1998; Fox, Marquis & Kipp 2000). For instance, mothers that are exposed to poor

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environmental conditions often produce offspring with lower fitness than mothers inhabiting a better environment (Bernardo 1996a, b; Mousseau & Fox 1998a; Kofman 2002; McCormick 2006). In addition, another problem in this field is that the interpretation of the adaptive significance of maternal effects is based on widely accepted hypotheses (e.g. environmental matching hypothesis) and derived notions and predictions, but does not focus on rigorous hypothesis testing or non-adaptive hypotheses. A more effective way to explore the adaptive significance of maternal effects is through a strong inference that involves multiple derivative variables, working hypotheses and full factorial design experiments to test these competing hypotheses (Huey & Berrigan 1996; Marshall 2008).

Maternal food availability can affect many traits (e.g. immune function, morphology, behaviour, growth, survival and sex), and in turn, the fitness of offspring (Kelly & Coutts 2000; Rutkowska & Cichon 2002; Suarez *et al.* 2009). Viviparous reptiles are excellent models for the study of the adaptive significance of maternal effects induced by food availability. In these species, the prolonged period of embryo retention in the uterus may provide the reproducing female an increased opportunity to influence embryonic developmental conditions (Shine 1995). In addition, in viviparous reptiles, the quantity of placental nutrient supply during embryogenesis is more likely to affect the offspring fitness (Fowden, Giussani & Forhead 2006). In this study, to identify the adaptive significance of the maternal effects, we conducted food manipulation experiments (high and low maternal food conditions × high and low offspring food conditions) and determined the effect of food treatments on the locomotor performance, growth and survival of offspring in a viviparous lacertid lizard (*Eremias multiocellata*). We predict several scenarios in which offspring may respond to the food conditions. First, the offspring would have a better performance in a food environment similar to that of their mother, as suggested by the environmental matching hypothesis (Monaghan 2008) (Fig. 1a). Second, the offspring under a maternal low-food condition would have an overall better performance, probably due to the compensation effect of the low-food condition, which is termed as low-food compensation hypothesis (Schew & Ricklefs 1998; Metcalfe & Monaghan 2001; Hector & Nakagawa 2012) (Fig. 1b). Third, the offspring under a maternal low-food condition would have an overall worse performance, probably due to the pathological effect of the low-food condition, which is termed as low-food pathology hypothesis; or due to a silver spoon effect that offspring from high-food maternal treatment did well (Dmitriew & Rowe 2011; Hopwood, Moore & Royle 2014) (Fig. 1c). Lastly, the performance of the offspring would not be affected by the maternal food condition, suggesting that no compensation exists, which is termed as no-compensation hypothesis (Fig. 1d).

Materials and methods

STUDY SITES AND ANIMALS

The experiments were conducted at Shierliancheng Field Station, Institute of Grassland Research of the Chinese Academy of Agricultural Sciences located in Jungar Banner, Inner Mongolia, China (40°12′17″N, 111°07′43″E; elevation 1036 m). This field station located in a desert steppe is characterized by cold semi-arid climate, with an average annual temperature of 6–7 °C and precipitation of 300–380 mm (http://www.nmic.gov.cn). The multi-ocellated racerunner (*Eremias multiocellata*), a small viviparous lizard (approximately 65 mm snout-vent length), is one of the main lizard fauna in this habitat, which is predominantly sandy grassland with low to moderate levels of sparse vegetation dominated by *Artemisia ordosica* (Zeng *et al.* 2014, 2016). Female *E. multiocellata* start to copulate in May, and give birth in July and August, with a gestation period of around two months (Zhang *et al.* 2010; Tang *et al.* 2012). The litter size of females from high-food conditions is larger than that of their counterparts from low-food conditions (3·7 vs. 2·7), but neonate body sizes are not affected by maternal food condition (Wang *et al.* 2017a).

EXPERIMENTAL DESIGN AND TREATMENTS

Briefly, we designed a factorial experiment (two maternal food treatments × two offspring food treatments) to identify the effect of maternal food conditions on female reproductive traits, as well as the effect of maternal and offspring food conditions on offspring traits.

Maternal food treatments

Adult *Eremias multiocellata* (24 males and 48 females) were collected near the field station during 20–30 May 2014. On 1 June, all females were measured [snout-vent length (SVL) and body mass] and were randomly allocated to 24 rounded enclosures (40 cm tall × 180 cm diameter) built in the field site, with one male and two females in each enclosure. The enclosures were covered with plastic nets to avoid bird predation. The 24 enclosures were evenly assigned to two treatments: maternal high-food (MHF) and low-food (MLF) treatments. A prior test of food intake indicated that the average consumption of mealworms for a gravid female was 0·04 g/g mass/day (range: 0·02–0·06 g/g mass/day). Accordingly, lizards in the high-food treatment were fed with 0·05 g mealworms/g mass/day (125% of the average food consumption of gravid females), and those in the low-food treatment were fed with 0·025 g mealworms/g mass/day (62·5% of the average food consumption of gravid females). The lizards were kept in these enclosures until the first hatchling was observed on 1 July. All females were then transferred to the laboratory at the field station to determine female reproductive output and offspring traits. In the laboratory, females were individually housed in a cage (31 cm long × 21 cm wide × 18 cm deep), containing a substrate of sand collected from the field site. The females were kept on the same feeding regimes and water every day ad libitum. A 10-h heating (from 08.00 to 18.00 h) was provided for behavioural thermoregulation by placing electric heating mats (25 W). Females produced a litter of offspring on 11·5 days in the high-food group, and 10·8 days in the low-food group (ranging from 5 to 20 days) after being moved to the laboratory.

Offspring food treatments

The cages were checked for neonates four times per day since the first parturition had occurred. Once found, the emerged neonates were collected and their SVL (to 0·01 mm) and body mass (to

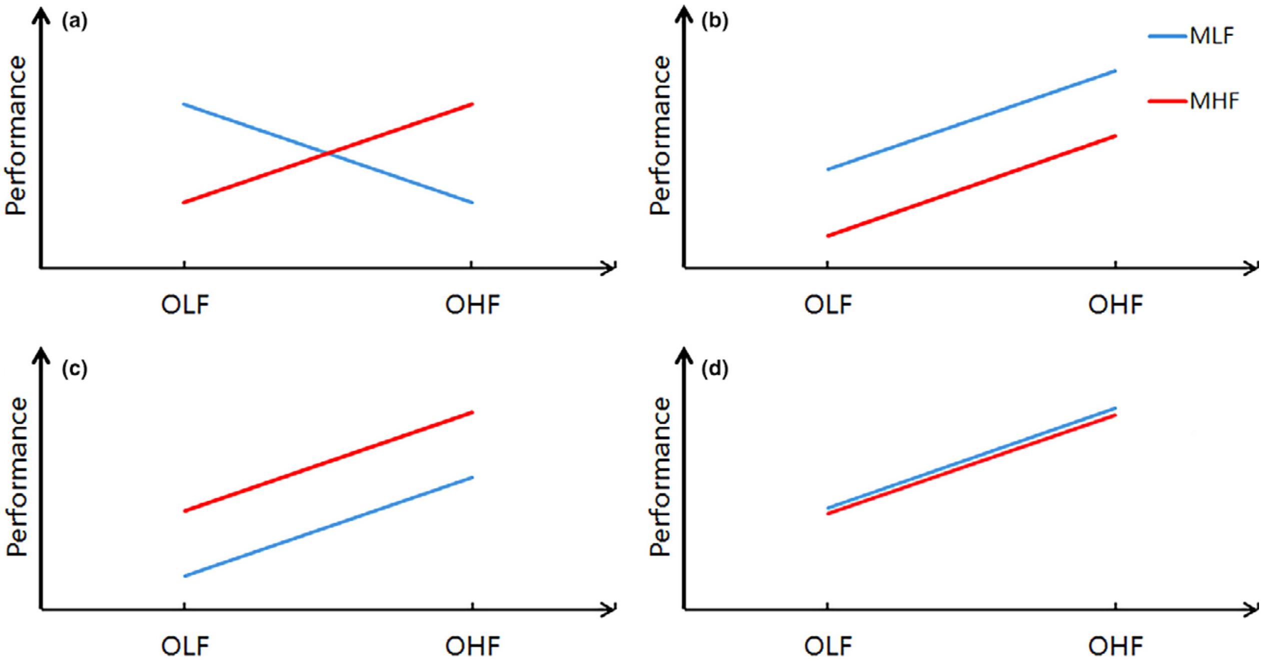

Fig. 1. A diagram of theoretical hypotheses on the responses of offspring to the maternal and offspring food conditions. (a) offspring would have a better performance under the food condition that match their mother's food condition, (b) offspring under maternal low-food condition would have a better performance overall, probably due to the compensation effect of the low-food condition, (c) offspring under maternal low-food condition would have a worse performance overall, probably due to the pathological effect of the low-food condition, (d) the performance of offspring would not be affected by the maternal food condition, suggesting no compensation exists. MHF, maternal high-food treatment; MLF, maternal low-food treatment; OHF, offspring high-food treatment; OLF, offspring low-food treatment.

0·001 g) were measured once the residual yolk was completely absorbed 1 day after hatching. The sex of neonates was identified by observing preanal scales. Males have large, square, regularly distributed preanal scales, while those of females are small, round and scattered (Wang *et al*. 2016). Neonates from each female were then randomly assigned to two offspring food conditions: high-food (OHF) and low-food (OLF) treatments. Neonates in the high-food treatment were fed with 0·05 g mealworms/g mass/day and those in the low-food treatment were fed 0·025 g mealworms/g mass/day for the same interval. Neonates (c. 15 individuals per cage) were marked with numbers on their back for identification and raised communally in cages (60 cm long × 43 cm wide × 34 cm deep) with a 3-cm-thick sand bed. The lizards from the same clutch were randomly assigned to two food availability treatment and, water was provided every day ad libitum. A 10-h heating was provided for behavioural thermoregulation (from 08.00 to 18.00 h, simulating the summer photoperiod at the collection site) by placing a 40-W incandescent bulb above one side of each cage. Lizard cages were placed on one of three different racks and were rotated twice a week to minimize positional effects.

LOCOMOTION, GROWTH AND SURVIVAL OF OFFSPRING

On day 30 after birth, each neonate was raced down a racetrack (100 cm long, marked at 20-cm intervals) by stimulating them with a soft paintbrush to measure locomotor performance (Irschick & Losos 1998). This procedure was repeated two times at 30 ± 1 °C with an hour break between each race. To quantify locomotor performance, we averaged the speed of the fastest 20-cm interval in each race as the sprint speed.

On day 30 after birth, neonates were re-measured for SVL (0·01 mm) and re-weighed (0·001 g). The growth rate of the neonates was calculated as the change in body mass and SVL divided by the number of days between measurements (30 days). Date of death for each offspring was recorded, and offspring survival was assessed once a day over a 2-month period after birth, by using stepwise cox regression analysis. The survival rate of lizards is low in the field during this period prior to winter (Warner & Shine 2007), and can thus be used as an important indicator of offspring fitness.

STATISTICAL ANALYSIS

All analyses were conducted using SPSS Statistics software (ver. 22; IBM Corp. 2013). Data were normalized by log-transformation when necessary. The effects of maternal and offspring food treatment (and their interaction) on growth and locomotion of offspring were evaluated by two-factorial mixed models, with maternal and offspring food availability as the independent variables and maternal identity (cage) as the random effect. The stepwise cox regression analysis was used to detect the effect of maternal and offspring food availability treatments on offspring survival.

Results

Maternal food condition significantly affected offspring growth in body mass, but not in SVL (Table 1; Fig. 2a,b). The growth rate of body mass was higher in the offspring under the MLF treatment than those under the MHF treatment (Fig. 2b). Offspring food condition significantly affected offspring growth in both body mass and SVL, with higher growth rates in the OHF treatment than in the OLF treatment (Table 1; Fig. 2a,b).

Table 1. Mixed model ANOVA results of the effects of maternal and offspring food conditions on growth and locomotor performance in neonatal *Eremias multiocellata*

Variable	Maternal food condition	Offspring food condition	Interaction
Growth in SVL	$F_{1,32}$ = 1·929, P = 0·114	$F_{1,32}$ = 5·958, **P = 0·020**	$F_{1,32}$ = 0·881, P = 0·355
Growth in Mass	$F_{1,32}$ = 5·715, **P = 0·023**	$F_{1,32}$ = 6·052, **P = 0·019**	$F_{1,32}$ = 1·439, P = 0·239
Sprint speed	$F_{1,22}$ = 4·807, **P = 0·039**	$F_{1,22}$ = 0·014, P = 0·908	$F_{1,22}$ = 1·585, P = 0·221

SVL, snout-vent length; BM, body mass.
P values in boldface are statistically significant.

Locomotor performance of neonates was not related to their body size (r^2 = 0·215, P = 1·76). Locomotor performance of neonates was affected by maternal food condition, but not by the food condition of offspring or the interaction between the maternal and offspring treatments (Table 1). Offspring produced by females under the MHF treatment ran faster than their counterparts under the MLF treatment (Fig. 2c).

Maternal food condition affected the survival of offspring, with higher survival rates for offspring under the MLF treatment than those under the MHF treatment (χ^2 = 6·054, P = 0·014; Fig. 3). Offspring food condition also affected their survival, with higher survival rates for offspring under the OHF treatment than those under the OLF treatment (χ^2 = 6·460, P = 0·011; Fig. 3). However, there was no significant interaction between maternal and offspring food conditions on offspring survival (χ^2 = 0·031, P = 0·861; Fig. 3). Taken together, the survival rate was highest in offspring under MLF treatment but raised under OHF treatment, and lowest for offspring under MHF treatment but raised under OLF treatment (Fig. 3).

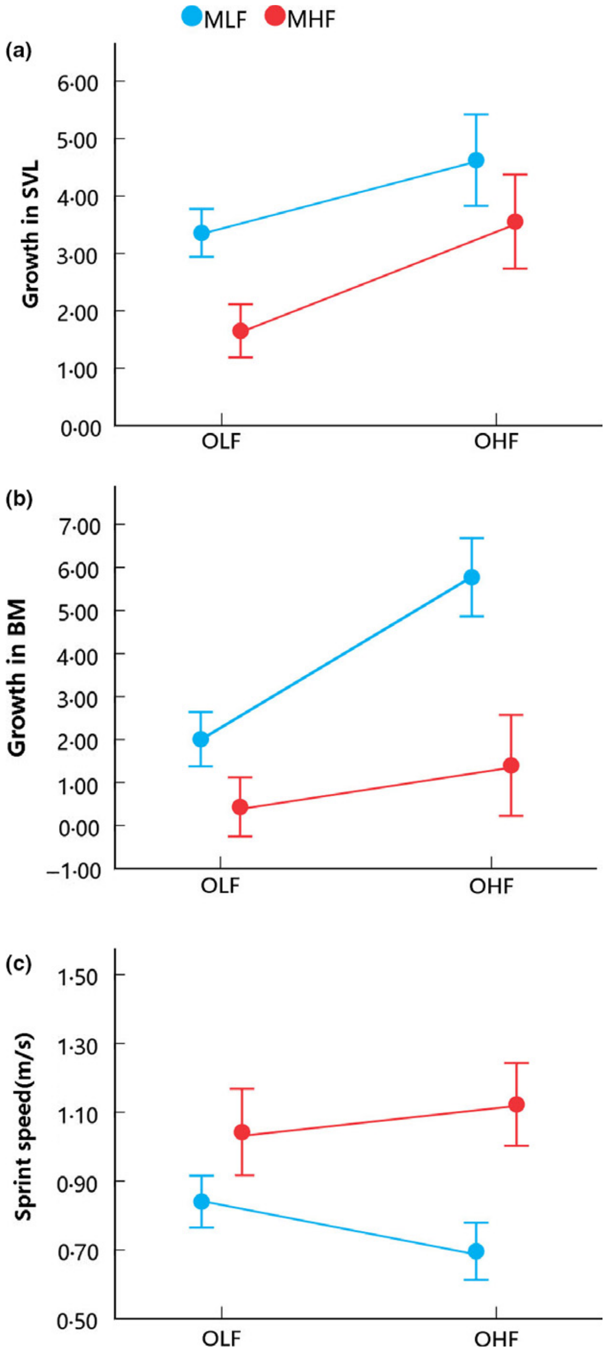

Fig. 2. Effects of maternal and offspring food condition on growth rate of snout-vent length (a), body mass (b) and locomotor performance (c) in neonatal *Eremias multiocellata*. Data are summarized as means ± SE. MHF, maternal high-food treatment; MLF, maternal low-food treatment; OHF, offspring high-food treatment; OLF, offspring low-food treatment.

Discussion

The environmental matching hypothesis is the dominant theory that explains the adaptive significance of maternal effects (Bernardo 1996a,b; Mousseau & Fox 1998b; Agrawal 2001). This hypothesis suggests that the maternal effect would be adaptive when the developmental conditions match post-developmental conditions, but detrimental when these conditions are mismatched. For example a mismatch of nutrient conditions in humans between the natal stage (nutrient-poor conditions) and the postnatal stage (nutrient-rich conditions) may lead to metabolic syndrome, cardiovascular diseases or type 2 diabetes (Hales & Barker 1992; Prentice 2005; Vaag *et al*. 2012). However, our study demonstrates that offspring under MLF conditions had better performance under all offspring food conditions to compensate for a bad start in their life. Anticipating a low-food condition by the mother appears to provide offspring fitness benefits, because the 'over-prepared' MLF-OHF offspring had the best performance of growth and survival, and the 'unprepared' MHF-OLF offspring had the worst. In contrast, anticipating a high-food condition does not seem to be important, because MHF-OHF offspring did not do better than MLF-OHF offspring in terms of growth and survival. That high-food mothers did not produce better offspring is presumably due to the limitation of maternal investment and the trade-off between offspring number

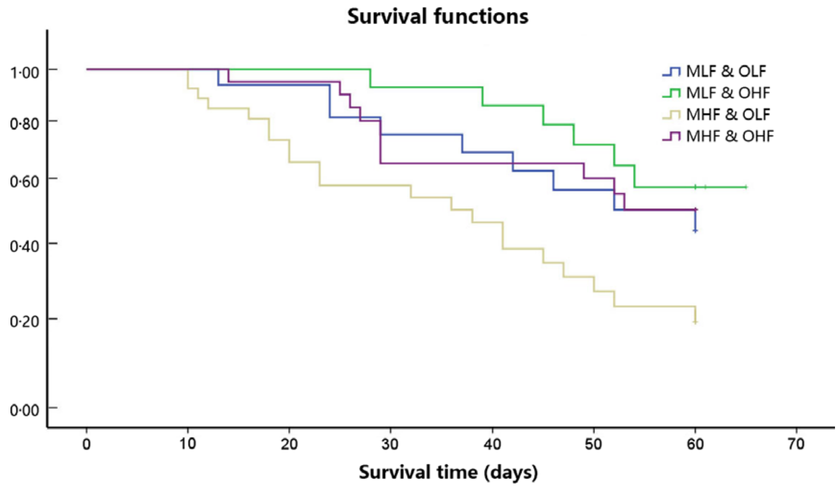

Fig. 3. Effects of maternal and offspring food condition on the mortality of neonatal *Eremias multiocellata*. MHF, maternal high-food treatment; MLF, maternal low-food treatment; OHF, offspring high-food treatment; OLF, offspring low-food treatment.

and size (Du, Ji & Shine 2005; Warne & Charnov 2008; Ji *et al*. 2009), given that females from high-food conditions produced more offspring rather than larger offspring with better performance (Wang *et al*. 2017a). Obviously, these results give clear support to the low-food compensation hypothesis rather than the environmental matching hypothesis. The phenomenon of low-food compensation has also been reported in other species. For example *Daphnia magna* females exposed to unfavourable conditions produced more resistant offspring than those under favourable conditions (Mitchell & Read 2005); many species of fish and birds showed compensatory growth after growth suppression due to complete or partial food deprivation (Ali, Nicieza & Wootton 2003; Giordano, Groothuis & Tschirren 2014).

The compensation to MLF conditions represents an example of 'predictive adaptive responses' (PARs), whereby a developing individual changes phenotypes as adaptive responses to environmental cues in early life stages, and gains benefits in later life stages with an anticipated environment (Gluckman, Hanson & Spencer 2005; Nettle, Frankenhuis & Rickard 2013). If the MLF condition is a forecast of postnatal food environment for offspring, it would be advantageous for MLF offspring to develop the phenotype of rapid growth that is appropriate for the anticipated OLF environment. This low-food compensation can be achieved mainly by maternal effects if the MLF offspring started with body sizes similar to those MHF offspring, or offspring plastic response if the MLF offspring started with a smaller body size (i.e. negative maternal effect) and subsequently caught up. Our study supports the first notion, because the body size of MLF offspring was similar to that of MHF offspring (Wang *et al*. 2017a). The underlying mechanism responsible for higher growth and survival rates of offspring under MLF conditions might be related to maternal programming of the physiological and biochemical parameters that influence energy metabolism and fat regulation (Hales & Barker 1992). For example individuals under poor nutrient environments may utilize energy more efficiently than those under nutrient-rich environments (Prentice 2005). This maternal programming of low-food compensation increased the performance of MLF offspring, but incurred a cost on the mother, with MLF females having poor postpartum body condition and immune function (Wang *et al*. 2017a).

Most of our results support the low-food compensation hypothesis, but the result on locomotor performance that is critical for the foraging and predation escaping of animals (Clemente & Wilson 2016; Scales & Butler 2016), supports the low-food pathology hypothesis. Lower locomotor performance in offspring under MLF conditions compared to those under MHF conditions, was likely due to (i) a direct and pathological effect of MLF condition on locomotive physiology, or (ii) the cost and trade-off of developmental plasticity. Mothers invested more energy and resources in ways that help offspring grow fast, but compromised the investment in the development of a locomotor system [e.g. muscles and/or appendages (Toscano, Manhaes-De-Castro & Canon 2008; Carmichael *et al*. 2012)]. For example under food stress, digestive organs such as the liver and gut could form at an earlier developmental stage or may grow larger (Kotrschal, Szidat & Taborsky 2014), which could be a developmental trade-off between locomotive organs and digestive organs. Similarly, reduced competitive fitness or reduced fecundity in *Drosophila melanogaster* acclimated to high temperatures, were interpreted as the representation of acclimation costs (Economos & Lints 1984; Jalal, Andersen & Hessen 2015). The higher growth in MLF offspring might enable them to out-grow predator vulnerability faster, and thus compensate for poorer running speed. Alternatively, the lower locomotor performance in MLF offspring is simply because MHF offspring have better locomotor performance due to a silver spoon effect (Hopwood, Moore & Royle 2014). Given the complexity of behavioural and physiological adjustments involved in phenotypic plasticity, including maternal effects, a single offspring fitness-related trait (e.g. locomotion) may not be sufficient to fully explain the adaptive significance of maternal effects, and even sometimes may mislead the interpretation. Therefore, we should measure multiple traits that are closely related to fitness, and more ideally, measure offspring fitness (for survival and reproduction) directly in studies that identify the adaptive significance of maternal effects. It must be considered that such studies require long-term experiments and are usually not feasible in most vertebrates with relatively long life span.

Previous studies have manipulated maternal food conditions to understand the maternally induced plasticity in offspring traits. For example females of *D. magna* could produce offspring of different sizes that subsequently differed in maturation time (Barata, Baird & Soares 2001); in brown anole lizards (*Anolis sagrei*), limited prey availability significantly reduced egg and offspring size and in turn, had decreased growth and survival rates (Warner & Lovern 2014). Such studies are important for identifying maternal effects and their potential fitness consequences, but contribute little to our understanding of the adaptive significance of maternal effects. A full factorial design is the most robust test for comparison of offspring fitness under different maternal and offspring food conditions to explore the adaptive significance of maternal effects (Warner *et al.* 2015). More generally, testing for multiple competing hypotheses involving both adaptive and non-adaptive explanations rather than a post hoc test of adaptive hypotheses should be routinely performed to study the adaptive significance of phenotypic plasticity (Huey & Berrigan 1996). Such an approach might ultimately provide critical insight into the evolution of many types of phenotypic plasticity, ranging from behavioural to physiological, and from short-term acclimation to transgenerational plasticity.

Authors' contributions

D.W.G. conceived the ideas and designed methodology; W.Y., L.S.R., Z.Z.G. and L.L. collected the data; W.Y. and D.W.G. analysed the data; D.W.G. and W.Y. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.s9b8d (Wang *et al.*, 2017b).

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