© 2024. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2024) 227, jeb246094. doi:10.1242/jeb.246094

REVIEW

SPECIAL ISSUE

DEVELOPMENTAL PLASTICITY: FROM MECHANISMS TO EVOLUTIONARY PROCESSES

Are parental condition transfer effects more widespread than is currently appreciated?

Matthew R. Walsh*, Anne Christian, Mikaela Feder, Meghan Korte and Kevin Tran

ABSTRACT

It has long been recognized that the environment experienced by parents can influence the traits of offspring (i.e. 'parental effects'). Much research has explored whether mothers respond to predictable shifts in environmental signals by modifying offspring phenotypes to best match future conditions. Many organisms experience conditions that theory predicts should favor the evolution of such 'anticipatory parental effects', but such predictions have received limited empirical support. 'Condition transfer effects' are an alternative to anticipatory effects that occur when the environment experienced by parents during development influences offspring fitness. Condition transfer effects occur when parents that experience high-quality conditions produce offspring that exhibit higher fitness irrespective of the environmental conditions in the offspring generation. Condition transfer effects are not driven by external signals but are instead a byproduct of past environmental quality. They are also likely adaptive but have received far less attention than anticipatory effects. Here, we review the generality of condition transfer effects and show that they are much more widespread than is currently appreciated. Condition transfer effects are observed across taxa and are commonly associated with experimental manipulations of resource conditions experienced by parents. Our Review calls for increased research into condition transfer effects when considering the role of parental effects in ecology and evolution.

KEY WORDS: Maternal effects, Transgenerational plasticity, Maternal condition, Silver spoon, Anticipatory effects

Introduction

Much research has demonstrated that the environment experienced by organisms during development can induce phenotypic changes that persist for multiple generations (Bashey, 2006; Jablonka and Raz, 2009; Bonduriansky et al., 2012; Salinas and Munch, 2012; Walsh et al., 2015, 2016; Bell and Hellmann, 2019; Donelan et al., 2020). This transgenerational plasticity occurs when the environment experienced by parents induces phenotypic changes in offspring and possibly future generations. One of the most prominent examples of a transgenerational response are 'maternal effects' or, more broadly, 'parental effects.' Parental effects manifest anytime the parental environment influences offspring phenotypes via impacts on offspring provisioning, hormones, behavior or epigenetic effects etc. (Bernardo, 1996; Grafen, 1988; Mousseau and Fox, 1998; Gustafsson et al., 2005; Marshall and Uller, 2007; Taborsky et al., 2007; Leips et al., 2009; Burton et al., 2020). A substantial amount of research has focused on the maternal role in parental effects and explored the extent to which mothers respond to predictable shifts in environmental conditions by modifying offspring phenotypes to best match future conditions (Uller et al., 2013). While there are clear examples of such 'anticipatory maternal effects' (Fig. 1A) (Agrawal et al., 1999; Galloway and Etterson, 2007; Salinas and Munch, 2012; Lind et al., 2020), the generality of this maternal effect remains unclear (Uller et al., 2013). This is because many organisms experience environmental conditions that theory predicts should favor the evolution of anticipatory effects (Marshall and Uller, 2007; Ezard et al., 2014; Kuijper and Hoyle, 2015; Leimar and McNamara, 2015; Uller et al., 2015) but a meta-analysis described the empirical evidence for anticipatory effects as 'weak' (Uller et al., 2013). What explains this disconnect between theory and the empirical literature?

'Condition transfer effects' represent an alternative class of parental effects that are less well studied than anticipatory effects (Bonduriansky and Crean, 2018). These effects occur when parents that experience high-quality conditions as they develop produce 'fitter' offspring across all environments that the offspring may encounter. Here, maternal and/or parental condition is 'transferred' to offspring such that there is a positive relationship between parental condition and offspring performance (Fig. 1B) (Bonduriansky and Crean, 2018; Bonduriansky, 2021). Silver spoon effects, where mothers that develop in high-quality habitats always produce higher-quality offspring, represent another term for a condition transfer effect (Grafen, 1988). Condition transfer effects represent a class of maternal effects that do not rely upon external environmental signals but are instead a byproduct of past environmental quality (Grafen, 1988; Van de Pol et al., 2006). Predictable shifts in environmental conditions will often covary with shifts in resources (or environmental quality etc.). Life history theory has long predicted that variation in resources is central to the evolution of maternal provisioning strategies (Charlesworth, 1980; Stearns and Koella, 1986; Kozlowski and Uchmanski, 1987; Kozlowski and Wiegert, 1987). Thus, condition transfer effects may provide an answer to the paradoxical lack of evidence for anticipatory maternal effects.

In this Review, we provide an overview of the current understanding of condition transfer effects in the literature. We specifically review studies that manipulate naturally occurring environmental stressors in the parental generation and then evaluate the fitness of offspring in response to exposure to that same stressor. We address three main questions: (1) Are condition transfer effects more widespread than is currently appreciated? (2) Which environmental stressors are most commonly associated with condition transfer effects? (3) Are there factors that influence the induction of condition transfer effects?

Background: maternal effects

Early interest in environmentally induced parental effects focused on the relationship between mothers and offspring (Bell and

Department of Biology, University of Texas at Arlington, Arlington, TX 76019, USA.

*Author for correspondence (matthew.walsh@uta.edu)

M.R.W., 0000-0002-7517-2013

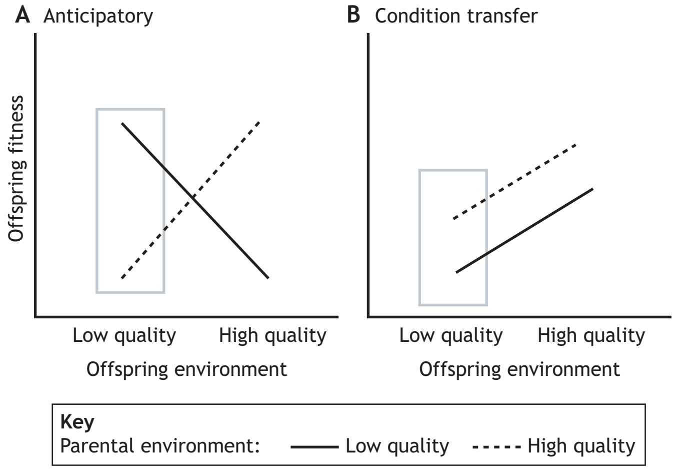

Fig. 1. Empirical evidence supporting anticipatory parental effects or parental condition transfer effects. (A) For anticipatory effects, the offspring of parents reared in environment A perform best in environment A (and vice versa). For this study, we focused on offspring fitness in the low-quality environment. If the offspring of parents from the low-quality environment exhibited higher fitness in the low-quality environment when compared with the offspring of parents from the high-quality environment, then this provides evidence for an anticipatory parental effect. (B) Condition transfer effects manifest as a significant main effect of parental environmental quality on offspring fitness and/or a positive relationship between parental condition and offspring performance. More importantly, if the fitness of offspring from high-condition parents exceeds the fitness of offspring of low-condition parents in the low-quality environment, then this supports a condition transfer effect. The grey boxes denote the treatments and comparisons that were made to distinguish between anticipatory versus condition transfer effects.

Hellmann, 2019). One form of a maternal effect is the connection between environmental quality, maternal provisioning of offspring, and offspring performance. Given that resources are typically limited for reproduction, it was recognized early on that selection should favor a balance between the production of many, small offspring versus the production of a few, large individuals (Lack, 1954; Smith and Fretwell, 1974). This led to the realization that spatial or temporal variation in environmental conditions may exert selection on patterns of maternal provisioning of offspring. In general, selection is expected to maximize maternal fitness as opposed to offspring fitness, especially in species that lack parental care and that reproduce many times (Marshall and Uller, 2007). As a result, there are several ways in which environmental conditions can modify the link between female and/or parental development and the traits of offspring. This includes the aforementioned anticipatory and condition transfer effects but also 'selfish' maternal effects that maximize maternal fitness at the expense of offspring fitness (Scheirs et al., 2000; Mayhew, 2001) and bet hedging (Shama, 2015; Tufto, 2015; Furness et al., 2015). Below, we provide a more thorough introduction into anticipatory effects and condition transfer effects as they are the focus of this Review.

Anticipatory parental effects

A substantial body of research has explored the extent to which maternal responses to environmental conditions enhance the fitness of offspring (reviewed by Marshall and Uller, 2007; Uller et al., 2013). These maternal effects are based upon the assumption that mothers 'anticipate' the environmental conditions that offspring will experience (i.e. high quality versus low quality, harsh versus benign, stressful versus non-stressful) and that they will then modify the phenotype of offspring accordingly (Marshall and Uller, 2007; Allen et al., 2008; Burgess and Marshall, 2014). Selection is expected to favor anticipatory maternal effects when: (1) environmental conditions shift predictably between generations, (2) cues reliably predict offspring conditions, and (3) the cost of maternal cue induction and transmission is low (Marshall and Uller, 2007). The empirical approach to studying anticipatory maternal effects typically utilizes factorial manipulations of maternal and offspring conditions. One example of a result supporting the existence of anticipatory maternal effects is evident by a significant maternal×offspring interaction such that offspring perform 'best' when reared in the same conditions that their mother experienced (Fig. 1A) (Dey et al., 2016). An additional possibility is that parents adjust the phenotype of offspring to an alternative environment when conditions change predictably between generations. The key result that supports the existence of an anticipatory response is that mothers that experience a low-quality or stressful environment will produce offspring with higher fitness than the offspring of mothers from high-quality environments when the offspring are exposed to the low-quality conditions (Fig. 1A). Some studies have provided clear evidence for the existence of anticipatory effects (Agrawal et al., 1999; Galloway and Etterson, 2007; Salinas and Munch, 2012; Lind et al., 2020).

Condition transfer effects

Condition transfer effects are maternal effects that are based upon the notion that an organism's condition reflects its quantity of energy reserves (Andersson, 1982; Rowe and Houle, 1996). One assumption is that 'high-condition' individuals have increased energy reserves, which, in turn, leads to the production of offspring with higher fitness. These maternal condition transfer effects then occur when investment in offspring quality is positively correlated with parental condition (Marshall and Uller, 2007; Bonduriansky and Crean, 2018). Here, high-condition parents 'transfer' their condition to offspring, and offspring from high-condition parents outperform offspring from low-condition parents regardless of the environment that offspring experience. This includes offspring of high-condition mothers having higher fitness especially in low-quality or stressful environments (Fig. 1B). Note that it may be possible to have a condition transfer effect and anticipatory effect operating at the same time if the effects of the environment on parents change over time (see Monaghan, 2008).

Condition transfer effects have historically received less attention than anticipatory effects (Bonduriansky and Crean, 2018; Bonduriansky, 2021). This is, in part, because researchers have considered condition transfer effects to represent a non-adaptive byproduct of parental quality. Yet, Bonduriansky and Crean (2018) made the important point that any form of parental effects will be adaptive if they increase parental (lifetime) reproductive success (see also Marshall and Uller, 2007). As a result, condition transfer effects have the potential to be adaptive because parents that experience high-quality conditions during development will likely produce offspring with higher fitness and/or produce more offspring throughout their lifetime (see Parker, 2002; Coulson and Porter, 1985; Ciconia, 2001; Van de Pol et al., 2006). In addition to being adaptive, condition transfer effects have the potential to be more widespread than anticipatory maternal effects. One reason is because anticipatory effects require the evolution of mechanisms (i.e. neural, sensory) that allow organisms to accurately receive and process environmental signals and modify the traits of offspring (Bonduriansky and Crean, 2018; Bonduriansky, 2021). In contrast, the expression and evolution of condition transfer effects more simply require a link between parental condition and investment in eggs/offsping and/or the transmission of factors that influence offspring performance (i.e. hormones, epigenetic effects). As a result, condition transfer effects are potentially more pervasive than is currently appreciated.

Review criteria

The main goal of this Review was to provide new insight into condition transfer effects. It was not intended to be comprehensive but instead highlight whether (or not) condition transfer effects are prevalent and worthy of further study. This Review also represents an extension of the earlier review on anticipatory maternal effects by Uller et al. (2013). This is because studies that manipulate environmental conditions during parent and offspring generations and thereby test for anticipatory effects can also test for condition transfer effects (see below). As a result, we first collated all of the papers that were included in Uller et al. (2013). We then used the same keyword search in ISI Web of knowledge as used by Uller et al. (2013). This search included the following terms: (maternal effect* OR parental effect* OR transgenera*plastic*) AND (experiment*) AND (environment*) AND (offspring OR fitness). This search was conducted in March 2023 and spanned the years 2011–2023. The key difference between anticipatory versus condition transfer effects relates to the fitness of offspring from parents exposed to stressful or low-quality conditions (Fig. 1). As a result, there were several criteria that we used when determining whether to include a paper in this Review. The criteria were: (1) the study reared the parental and offspring generation on contrasting environmental conditions (or a range of conditions). (2) We were able to classify one of the environments as low quality or stressful. This is important because studies that imposed stressful treatments would be more likely to generate parents of contrasting condition. This would, in turn, allow us to better distinguish anticipatory versus condition transfer effects. This eliminated studies that, for instance, manipulated temperature but did not specify whether the increase or decrease in temperature was likely to be stressful. (3) The study assessed the fitness of offspring in the low-quality or stressful environment. This allowed us to determine if high-condition parents transfer their condition to offspring in low-quality conditions. The lone exception is that we did include two studies that exposed a parental generation to predator cues but did not manipulate the offspring generation. (4) The study manipulated a naturally occurring environmental stressor. This eliminated studies that involved, for instance, hormone manipulations.

Based upon these search parameters and criteria, this Review included 55 papers. We defined specific criteria for results supporting anticipatory versus condition transfer effects. We considered a paper as providing evidence for anticipatory effects when the offspring of mothers or parents from the low-quality or stressful environment had higher fitness in the low-quality environment when compared with fitness of offspring from mothers/parents from the high-quality environment (Fig. 1A). The opposite trend (mothers or parents from high-quality environments producing more fit offspring) instead provided evidence for condition transfer effects (Fig. 1B). It is also possible for studies to provide evidence for both anticipatory and condition transfer effects. This is, in part, because it is difficult to design experiments that will unambiguously tease apart anticipatory effects from condition transfer effects as both could be operating simultaneously (Enqqvist and Reinhold, 2016). Studies could provide evidence for both forms of parental effects if one trait provides evidence for an anticipatory effect while another trait is consistent with the criteria for a condition transfer effect. Also note that the expression of parental effects can be influenced by contributions from mothers and fathers. As a result, we also tracked whether studies exposed one or both parents and also whether studies were able to disentangle parental effects due to mothers versus fathers (see Table 1).

Evidence for condition transfer effects

There is widespread evidence for condition transfer effects (Table 1). Greater than 50% (29/55 studies) of the empirical studies included in this review observed evidence for condition transfer effects (Table 1). In such studies, there was at least one example where the trait value of the offspring of parents that experienced high-quality conditions exceeded the trait values of offspring of parents that experienced low-quality conditions when the offspring were in the stressful environment (Fig. 1B). That is, the fitness of offspring of high-condition parents was higher than the fitness of offspring of low-condition parents in the low-quality or stressful environment. The evidence for condition-dependent transfer effects is taxonomically diverse as there are examples in plants, aquatic invertebrates, terrestrial invertebrates, fish and reptiles (Table 1). Furthermore, we identified 35 studies that manipulated resource quality or quantity (Table 1). This included studies that directly manipulated resources (or water for plants) or proxies for resources such as density. Condition transfer effects were more commonly observed (21/35 or 60%) than anticipatory effects (16/35=46%) in such studies. Some studies that manipulated resources revealed very clear cases of condition transfer effects. For example, Bonduriansky and Head (2007) manipulated larval diet quality in the parent and offspring generations in the fly (*Telostylinus angusticollis*). They showed that high-condition mothers produced offspring that developed faster on the low-quality food treatment when compared with the offspring of low-condition mothers. Similarly, Beyer and Hambright (2017) reared multiple generations of rotifers (*Brachionus calyciflorus*) on high-quality (*Chlamydomonas*) versus low-quality (*Microcystis*) algae and found that the offspring of mothers fed high-quality food had higher fitness (intrinsic rate of increase) on the low-quality food when compared with the offspring of mothers fed *Microcystis*.

The studies that document condition transfer effects are not limited to manipulation of resources (Table 1). Of the 20 studies that manipulated environmental factors other than resources, 7/20 (35%) detected evidence for condition transfer effects. For example, Fernández-González et al. (2011) exposed water fleas (*Daphnia magna*) to sub-lethal concentrations of copper. The offspring of parental *Daphnia* that were not exposed to copper were larger and produced more offspring compared with the offspring of parents that were exposed to copper. Such differences were only apparent when the offspring were exposed to copper. In a separate study on *Daphnia magna*, Mikulski and Pijanowska (2017) found that mothers that were exposed to fish predator kairomones produced offspring that were smaller at maturation and exhibited lower reproductive investment when compared with offspring from control mothers (when the offspring generation was reared in the presence of predator cues).

It was not uncommon for studies to document the presence of condition transfer effects for one trait but an anticipatory response for another trait (Table 1). Wang et al. (2017) manipulated resource availability in the lizard (*Eremias multiocellata*) and observed that the offspring of high-condition mothers (i.e. fed high food levels) exhibited a faster sprint speed on low food compared with the offspring of low-condition mothers, clearly showing a condition transfer effect. Conversely, the offspring of low-condition mothers grew faster on low food when compared with the growth rates of

Table 1. Summary of the empirical studies on parental effects across vertebrates, invertebrates and plants included in this Review

Organism	Species	Stressor	Trait	Parental manipulation	Timing of exposure	Reference
Condition transfer parental effects						
Beetle	*Stator limbatus*	Resource quality	Life history	Both	Juvenile	Fox et al., 1995
Water flea	*Daphnia pulex*	Copper exposure	Life history	Maternal	Juvenile	Fernández-González et al., 2011
Fly	*Telostylinus angusticollis*	Resource quality	Life history	Both*	Juvenile	Bonduriansky and Head, 2007
Beetle	*Caryedon palaestinicus*	Resource quality	Life history	Maternal	Juvenile	Or and Ward, 2007
Beetle	*Tachyporus hypnorum*	Resource quality	Life history	Maternal	Juvenile	Kyneb and Toft, 2006
Aphid	*Aphis nerii*	Resource quality, density	Life history	Maternal	Juvenile	Hayden et al., 2021
Rotifer	*Brachionus calyciflorus*	Resource quality	Life history	Maternal	Juvenile	Zhou and Declerck, 2020; Beyer and Hambright, 2017
Mosquito	*Aedes aegypti*	Resource quality	Life history	Both	Juvenile	Zirbel et al., 2018
Fruit fly	*Drosophila melanogaster*	Resource quality	Life history	Both	Juvenile	Vijendravarma et al., 2010
Water flea	*Daphnia magna*	Resource quality	Life history	Maternal	Juvenile	Radersma et al., 2018
		Predator cue	Life history	Maternal	Juvenile	Mikulski and Pijanowska, 2017
Snail	*Lymnaea stagnalis*	Temperature	Life history	Maternal	Adult	Leicht and Seppälä, 2019
Aphid	*Aphis nerii*	Density	Life history	Maternal	Juvenile	Zehnder and Hunter, 2007
Plant	*Erodium cicutarium*	Resource availability	Life history	Maternal	Juvenile	Jacobs and Lesmeister, 2012
Plant	*Lupinus angustifolius*	Water availability	Life history	Maternal	Juvenile	Matesanz et al., 2022
Plant	*Hieracium umbellatum*	Water availability	Life history	Maternal	Juvenile	Ehlers et al., 2018
Stickleback	*Gasterosteus aculeatus*	Salinity	Life history	Both	Juvenile	Heckwolf et al., 2018
Anticipatory parental effects						
Butterfly	*Pieris rapae*	Resource quality	Life history	Both	Juvenile	Rotem et al., 2003
Mosquito	*Anopheles stephensi*	Resource availability	Life history	Both	Juvenile	Grech et al., 2007
Springtail	*Orchesella cincta*	Resource availability	Life history	Both*	Juvenile	Zizzari et al., 2016
Water flea	*D. magna*	Resource availability/density	Parasite resistance	Maternal	Juvenile	Mitchell and Read, 2005
Copepod	*Tigriopus japonicus*	Copper exposure	Life history	Maternal	Juvenile	Kwok et al., 2009
Cricket	*Gryllus pennsylvanicus*	Predator cue	Behavior	Maternal	Adult	Storm and Lima, 2010
Earwig	*Forficula auricularia*	Resource availability	Life history	Maternal	Juvenile	Raveh et al., 2016
Beetle	*Tenebrio molitor*	Pathogen exposure	Life history	Both	Juvenile	Moret, 2006
Water flea	*Daphnia cucullata*	Predator cue	Morphology	Maternal	Juvenile	Agrawal et al., 1999
Butterfly	*Melitaea cinxia*	Resource availability	Life history	Maternal	Juvenile	Saastamoinen et al., 2013
Snail	*Physa acuta*	Predator cue	Behavior	Both*	Juvenile	Tariel et al., 2020
Plant	*Raphanus raphanistrum*	Herbivore exposure	Herbivore resistance	Maternal	Juvenile	Agrawal et al., 1999
Plant	*Secale sylvestre*	Water availability	Life history	Maternal	Juvenile	Mojzes et al., 2021
Lizard	*Niveoscincus ocellatus*	Resource quality	Life history	Maternal	Adult	Cadby et al., 2011
Lizard	*Anolis sagrei*	Resource availability	Life history	Maternal	Adult	Warner et al., 2015
Bird	*Parus major*	Parasite exposure	Physiology	Maternal	Adult	De Coster et al., 2012
Both condition transfer and anticipatory parental effects						
Bryozoan	*Bugula neritina*	Copper exposure	Life history	Maternal	Adult	Marshall, 2008
Snail	*Nucella lapillus*	Predator cue	Life history	Both	Adult	Donelan and Trussell, 2018
Beetle	*Neolema abbreviata*	Resource quality	Life history	Both	Juvenile	Mbande et al., 2020
Plant	*Taraxacum brevicorniculatum*	Density	Life history	Maternal	Juvenile	Puy et al., 2021
Plant	*Polygonum persicaria*	Density	Life history	Maternal	Juvenile	Waterman and Sultan, 2021
		Water availability	Life history	Maternal	Juvenile	Sultan et al., 2009
Plant	*Centaurea hyssopifolia*	Habitat quality/ water availability	Life history	Maternal	Juvenile	Pías et al., 2010
Plant	*Plantego lanceolata*	Nutrient availability	Life history	Maternal	Juvenile	Latzel et al., 2010
Lizard	*Eremias multiocellata*	Resource availability	Life history	Maternal	Adult	Wang et al., 2017
Guppy	*Poecilia reticulata*	Resource availability	Life history	Maternal	Juvenile	Bashey, 2006
		UV radiation	Physiology	Both	Adult	Ghanizadeh Kazerouni, et al., 2017

Continued

Table 1. Continued

Organism	Species	Stressor	Trait	Parental manipulation	Timing of exposure	Reference
No parental effects						
Springtail	*Folsomia candida*	Resource availability	Life history	Maternal	Juvenile	Hafer et al., 2011
Water flea	*D. magna*	Resource availability	Life history	Maternal	Juvenile	Coakley et al., 2018
		Resource quality	Life history	Maternal	Juvenile	Gustafsson et al., 2005
Aphid	*Myzus persicae*	Parasitoid exposure	Parasitoid resistance	Maternal	Juvenile	Vorburger et al., 2008
Spider	*Erigonedentipalpis*	Resource availability	Life history	Both	Juvenile	Mestre and Bonte, 2012
Fruit fly	*D. melanogaster*	Pathogen exposure	Life history	Maternal	Juvenile	Nystrand et al., 2016
Plant	*R. raphanistrum*	Herbivore exposure	Herbivore resistance	Maternal	Juvenile	Agrawal, 2002
Bird	*P. major*	Predator exposure	Life history	Maternal	Adult	Coslovsky and Richner, 2012
Lizard	*Eremias argus*	Humidity	Life history	Both	Adult	Wang et al., 2021
Lizard	*Liopholis whitii*	Resource availability	Life history	Maternal	Adult	Botterill-James et al., 2019

The ‘Parental manipulation’ column indicates which parents were exposed to the environmental stressor; maternal or both maternal and paternal (Both). *Study used an experimental design that disentangled phenotypic effects on offspring due to mothers versus fathers. The ‘Timing of exposure’ column indicates whether the environmental stressor was imposed when parents were juveniles or adults.

high-condition mothers, indicating an anticipatory effect. Sultan et al. (2009) observed contrasting responses to drought stress in two closely related species of plants. In one species (*Polygonum persicaria*), drought stressed parents produced offspring with longer roots and larger seedling biomass in dry soil versus plants from parents grown in moist soil. Such results support an anticipatory response. In *Polygonum hydropiper*, the offspring of drought stressed parents had shorter roots and were smaller in dry soil, which is consistent with a condition transfer effect (non-stressed parent produced offspring with higher fitness). Given that *P. persicaria* is found in moist and dry sites whereas *P. hydropiper* is limited to moist sites, these results also indicate that contrasting ecological conditions may favor distinct forms of maternal effects.

The evidence for condition transfer effects was, of course, not universal. Several studies did not find any evidence for condition transfer effects or anticipatory maternal effects (Table 1). In some cases, this does not mean that these studies did not reveal any maternal effects but instead did not find evidence for anticipatory or condition transfer effects as defined in the review criteria for this study (see Coslovsky and Richner, 2012; Coakley et al., 2018; Botterill-James et al., 2019; Mojzes et al., 2021). For instance, Botterill-James et al. (2019) manipulated resource availability during gestation and found that low-condition mothers (i.e. fed low food) produced offspring that grew faster than offspring from high-condition mothers. However, such differences were only observed when the offspring were fed high food; no differences in growth were found on low food. In other cases, the evidence for parental effects was largely absent. Vorburger et al. (2008) showed that parental exposure to parasitoids in the aphid (*Myzus persicae*) yielded maternal effects that were weak or absent.

Quantifying parental effects in offspring

In addition to qualitatively summarizing the evidence for condition transfer effects, we also examined the magnitude of condition transfer effects. For any given trait that provided evidence for a significant parental effect, we calculated the magnitude of such an effect for the offspring generation exposed to low-quality conditions via the following formula: absolute value [(offspring of parent from low-quality treatment–offspring of parent from high-quality environment)/average offspring trait value] (see Table S1). These data were extracted using the figure calibration plugin for ImageJ (NIH). For all of the cases that provided evidence for a significant condition transfer effect, the offspring of parents that experienced high-quality conditions exhibited trait values that should enhance fitness compared with the offspring of parents that were exposed to low-quality conditions (i.e. faster development, larger body size, faster growth etc.). The same is true for the studies that yielded significant evidence for anticipatory effects. As a result, this quantitative approach is a proxy for the magnitude of the fitness advantages associated with distinct forms of parental effects.

This approach yielded strong effects associated with anticipatory and condition transfer effects (Fig. 2). The average treatment effects in the offspring generation were 32% and 41% for condition transfer and anticipatory effects, respectively (Fig. 2A). This means that for condition transfer effects the average difference in offspring trait values in the low-quality environment was 32% between the offspring from parents that experienced high versus low-quality conditions. Because resource-related manipulations were the most common treatment utilized by the studies included in this Review (Table 1) and also because resources are likely important to condition transfer effects, we also evaluated these same trends for studies that manipulated resources. This broadly included studies that altered resource levels, resource quality, density and water availability for plants. The trends were similar (see Fig. 2B). It is important to note that we quantified the magnitude of parental effects only for results that provided an example (based upon non-overlapping error bars) of anticipatory (or condition transfer) effects in a subset of the offspring treatments (offspring in the low-quality treatments). Our results show that when studies revealed evidence for a significant parental effect (whether it be condition transfer or an anticipatory effect), the magnitude of the effect was strong. However, the vast majority of studies quantify maternal effects for several traits and did not find evidence for anticipatory (condition transfer) effects for all or even the majority of traits. Thus, the average magnitude of any effect would be weaker if the traits that yielded negative results were also included in our results. Given that Uller et al. (2013) performed a meta-analysis that included all results, this can help to explain why they observed overall weak evidence for anticipatory maternal effects.

When and why are condition-dependent transfer effects likely to be observed?

We examined the papers that are included in this study to determine if there are commonalities that will predict when and why we might

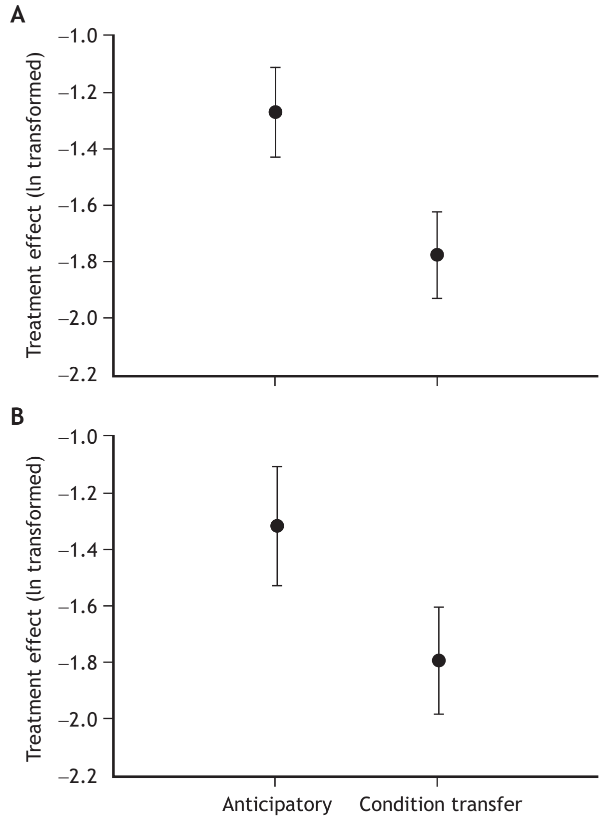

Fig. 2. Magnitude of condition transfer versus anticipatory effects. (A) All studies. (B) Studies that manipulated resource availability. Data are means±s.e.m. of n=46 (anticipatory) and n=49 (condition transfer). Each panel displays the average treatment effect [(differences in offspring trait values in the low-quality environment)/trait mean].

observe condition transfer effects. One immediate trend that is apparent is that condition-dependent transfer effects are common in studies that manipulate parental and offspring resource availability and/or resource quality (also water availability in plants) (Table 1). For instance, of the 29 papers that provided some evidence for condition transfer effects, >75% (22/29) of them directly or indirectly modified resources. This is not necessarily surprising given that the amount or quality of resources experienced by parents will directly influence their ability to provision offspring. Thus, variation in resource levels or quality appears to be a key determinant of the expression of condition transfer effects.

In addition to the type of stressor that influences the expression of maternal effects, we also considered whether there are specific early life advantages that best predict the occurrence of condition transfer effects. In particular, are condition transfer effects simply a byproduct of differences in egg or offspring size? Does parental exposure to low-quality or stressful conditions lead to the production of smaller offspring (and vice versa for high-condition parents)? This does not appear to be the case. While there are examples of high-condition mothers producing larger eggs or offspring (Kyneb and Toft, 2006; Bonduriansky and Head, 2007; Or and Ward, 2007; Matesanz et al., 2022), there are also examples showing that low-condition mothers produce larger eggs/offspring (Beyer and Hambright, 2017; Zhou and Declerck, 2020). Other studies that provided evidence for condition transfer effects did not find any connection between maternal condition and egg or offspring size (Fernández-González et al., 2011; Ehlers et al., 2018; Radersma et al., 2018). It is thus clear that condition transfer effects can provide a link between parental condition and offspring fitness irrespective of an influence on egg or offspring size per se.

The empirical studies often varied in the timing and/or duration of exposure to an environmental stressor. For example, some studies reared parents/offspring in the presence and absence of the stressor for their entire lives while others exposed organisms for shorter periods of time or during discrete life history phases. We evaluated the studies included in this review and listed whether the environmental stressor was imposed when the parents were juveniles versus adults (see Table 1). One apparent trend is that the vast majority of studies that detected condition transfer effects exposed the parental generation to the environmental stressor early in life (as juveniles) (Table 1; 86% or 25/29 of the studies). It is intuitive that the timing and duration of exposure may influence the ability to detect condition transfer effects as exposure to a stressful condition early in life may increase the differences in condition between the low- and high-quality environmental conditions. However, it is also important to note that most studies we consider in this Review exposed juveniles to the stressor in the parental generation (as opposed to the adult stage) (43/55 studies). Thus, the relative importance of exposure early versus later in life in terms of the induction of parental effects is less clear based upon the studies we included.

Condition-dependent transfer effects in the wild

We have largely focused on condition-dependent transfer effects in a laboratory setting. However, it is important to emphasize that condition transfer effects have been observed in captive populations (Parker, 2002), in correlational studies in natural populations (Coulson and Porter, 1985; Ciconia, 2001; Van de Pol et al., 2006) and in field experiments (Gagliano and McCormick, 2007; Allen et al., 2008; Giordano et al., 2014; Burton et al., 2020). For example, increased body condition is associated with increased clutch size in birds (Ciconia, 2001). High parental condition can also have long term fitness consequences. In a 20-year mark–recapture study, developing in a high-quality habitat and increased parental condition was shown to significantly increase lifetime reproductive success in oystercatchers (*Haematopus ostralegus*) (Van de Pol et al., 2006). In an experimental study on a coral reef fish (*Pomacentrus amboinensis*), Gagliano and McCormick (2007) showed that high-condition females (due to food supplementation) provisioned eggs with increased energy reserves. Eggs with larger yolk sacs were more likely to hatch and the subsequent offspring exhibited higher survival. There is thus good evidence that condition transfer effects occur in more natural situations.

Conclusions and future directions

Our Review argues that condition transfer effects are indeed more widespread than is currently appreciated. This supports the predictions of previous researchers regarding the underrealized importance of condition transfer effects (Bonduriansky and Crean, 2018). We found evidence for condition transfer effects across a variety of taxa and environmental stressors (Table 1). Although there are studies that document condition transfer effects in response to several environmental stressors (Table 1), the majority of examples of condition transfer effects involved parental manipulations of resource availability or resource quality (or water availability for plants) (Table 1). Such results signal that condition transfer effects may be less likely to be driven by external environmental signals but could instead be more strongly determined by factors that dictate parental condition. This trend is not particularly surprising given that condition transfer effects rely upon females or parents differing in condition which should be linked to the resources that they experience during development. With that said, we feel there are several outstanding avenues of future research.

Maternal versus paternal effects

Our Review collated information on whether one or both parents were exposed to the environmental stressors (Table 1). This is important because offspring development can be influenced by environmental effects on mothers as well as fathers (Bonduriansky and Head, 2007; Zizzari et al., 2016; Tariel et al., 2020). For example, the parental influence on offspring escape behavior in freshwater snail (*Physa acuta*) depended upon whether mothers or fathers were exposed to predator cues (Tariel et al., 2020). Such a result is important because we included just three papers that utilized experimental designs that could quantify the relative importance of maternal versus paternal effects on offspring fitness (Table 1). As a result, an increased understanding of the relative contributions of maternal versus paternal effects in the context of transgenerational plasticity should be a priority for future research.

Mechanisms of condition transfer effects

Condition transfer effects do not appear to manifest because of a simple connection between maternal resource availability during development and shifts in egg or offspring size (see above). Several studies explicitly made the point that offspring size does not predict offspring fitness (see Beyer and Hambright, 2017). Increased attention to how and why differences in maternal or paternal condition yields differences in offspring fitness is warranted. This includes a better understanding of the underlying hormonal, physiological, and non-genetic mechanisms of condition transfer effects.

Induction of condition transfer effects

Our Review provided some evidence that the duration of exposure may be important to the induction of condition transfer effects (see above). The majority of studies that provided evidence for condition transfer effects manipulated the environmental stressor when parents were young. Yet, this approach was not universal (Table 1). More work is needed to better understand when condition transfer effects are likely to manifest in wild populations. In particular, a better understanding of how the timing, magnitude and duration of environmental stressors induce condition transfer effects is needed.

Taxonomic bias

The studies included in this Review were skewed towards the use of invertebrates as study organisms (34/55 studies, 62%). This likely stems from the experimental advantages of using organisms that are small and display a short generation time when conducting multi-generation experimental studies. This Review included just 10 studies that used vertebrate species. Furthermore, most of these studies on vertebrates exposed the parental generation to an environmental stressor when they were adults (8/10 studies). Experimental studies that examine parental effects in vertebrates when such organisms experience low-quality conditions early in life or throughout development are lacking and should be a priority for future research.

Fitness consequences of condition transfer effects.

We provided evidence that condition transfer exists and may influence fitness in natural populations (Coulson and Porter, 1985; Ciconia, 2001; Van de Pol et al., 2006). However, more experiments in nature across a broader range of taxa would be beneficial to determine the broad ecological importance of condition transfer effects.

Evolution of condition transfer effects

A small number of studies provided evidence for interpopulation or interspecific differences in the degree or forms of maternal effects (e.g. Bashey, 2006; Sultan et al., 2009). In these examples, the populations/species originated from contrasting environments. Such results foreshadow that there may be specific ecological conditions that favor the evolution of condition transfer effects. As a result, more work is needed from both a theoretical and empirical perspective to determine the ecological conditions that drive the evolution of condition transfer effects.

Acknowledgements
M.R.W. thanks Katie Gilmour and Pat Wright for the invitation to the JEB 2023 symposium and for the Company of Biologists for providing funding for the symposium. M.R.W. would also like to thank all of the participants for stimulating presentations and discussions.

Competing interests
The authors declare no competing or financial interests.

Funding
M.R.W. was funded by the National Science Foundation while preparing this manuscript (IOS-1651613, DEB-2028775, DEB-2236741).

Special Issue
This article is part of the Special Issue ‘Developmental plasticity: from mechanisms to evolutionary processes’, guest edited by Patricia A. Wright and Kathleen M. Gilmour. See related articles at https://journals.biologists.com/jeb/issue/227/Suppl_1

References

Agrawal, A. (2002). Herbivory and maternal effects: mechanisms and consequences of transgenerational induced plant resistance. *Ecology* **83**, 3408-3415. doi:10.1890/0012-9658(2002)083[3408:HAMEMA]2.0.CO;2

Agrawal, A. A., Laforsch, C. and Tollrian, R. (1999). Transgenerational induction of defences in animals and plants. *Nature* **401**, 60-63. doi:10.1038/43425

Allen, R. M., Buckley, Y. M. and Marshall, D. J. (2008). Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am. Nat.* **171**, 225-237. doi:10.1086/524952

Andersson, M. (1982). Sexual selection, natural selection and quality advertisement. *Biol. J. Linn. Soc.* **17**, 375-393. doi:10.1111/j.1095-8312.1982.tb02028.x

Bashey, F. (2006). Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy *Poecilia reticulata*. *Evolution* **60**, 348-361.

Bell, A. M. and Hellmann, J. K. (2019). An integrative framework for understanding the mechanisms and multigenerational consequences of transgenerational plasticity. *Annu. Rev. Ecol. Evol. Syst.* **50**, 97-118. doi:10.1146/annurev-ecolsys-110218-024613

Bernardo, J. (1996). Maternal effects in animal ecology. *Am. Zool.* **36**, 83-105. doi:10.1093/icb/36.2.83

Beyer, J. E. and Hambright, K. D. (2017). Maternal effects are no match for stressful conditions. *Funct. Ecol.* **31**, 1933-1940. doi:10.1111/1365-2435.12901

Bonduriansky, R. (2021). Plasticity across generations. In *Phenotypic Plasticity & Evolution*, pp. 327-348. CRC Press.

Bonduriansky, R. and Crean, A. J. (2018). What are parental condition-transfer effects and how can they be detected? *Methods Ecol. Evol.* **9**, 450-456. doi:10.1111/2041-210X.12848

Bonduriansky, R. and Head, M. (2007). Maternal and paternal condition effects on offspring phenotype in *Telostylinus angusticollis* (Diptera: Neriidae). *J. Evol. Biol.* **20**, 2379-2388. doi:10.1111/j.1420-9101.2007.01419.x

Bonduriansky, R., Crean, A. J. and Day, T. (2012). The implications of nongenetic inheritance for evolution in changing environments. *Evol. Appl.* **5**, 192-201. doi:10.1111/j.1752-4571.2011.00213.x

Botterill-James, T., Munch, K. L., Halliwell, B., Chapple, D. G., Gardner, M. G., Wapstra, E. and While, G. M. (2019). Low food availability during gestation enhances offspring post-natal growth, but reduces survival, in a viviparous lizard. *Oecologia* **189**, 611-620. doi:10.1007/s00442-019-04349-5

Burgess, S. C. and Marshall, D. J. (2014). Adaptive parental effects: the importance of estimating environmental predictability and offspring fitness appropriately. *Oikos* **123**, 769-776. doi:10.1111/oik.01235

Burton, T., Rollinson, N., McKelvey, S., Stewart, D. C., Armstrong, J. D. and Metcalfe, N. B. (2020). Adaptive maternal investment in the wild? Links between maternal growth trajectory and offspring size, growth, and survival in contrasting environments. *Am. Nat.* **195**, 678-690. doi:10.1086/707518

Cadby, C. D., Jones, S. M. and Wapstra, E. (2011). Potentially adaptive effects of maternal nutrition during gestation on offspring phenotype of a viviparous reptile. *J. Exp. Biol.* **214**, 4234-4239. doi:10.1242/jeb.057349

Charlesworth, B. (1980). *Evolution in Age-Structured Populations*. Cambridge, U.K: Cambridge Univ. Press.

Ciconia, C. (2001). Condition-dependent parental effort and reproductive performance in the white stork. *Ardea* **89**, 2.

Coakley, C. M., Nestoros, E. and Little, T. J. (2018). Testing hypotheses for maternal effects in *Daphnia magna*. *J. Evol. Biol.* **31**, 211-216. doi:10.1111/jeb.13206

Coslovsky, M. and Richner, H. (2012). Preparing offspring for a dangerous world: potential costs of being wrong. *PLoS ONE* **7**, e48840. doi:10.1371/journal.pone.0048840

Coulson, J. C. and Porter, J. M. (1985). Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* **127**, 450-466. doi:10.1111/j.1474-919X.1985.tb04841.x

De Coster, G., De Neve, L., Verhulst, S. and Lens, L. (2012). Maternal effects reduce oxidative stress in female nestlings under high parasite load. *J. Avian Biol.* **43**, 177-185. doi:10.1111/j.1600-048X.2012.05551.x

Dey, S., Proulx, S. R. and Teotónio, H. (2016). Adaptation to temporally fluctuating environments by the evolution of maternal effects. *PLoS Biol.* **14**, e1002388. doi:10.1371/journal.pbio.1002388

Donelan, S. C. and Trussell, G. C. (2018). Parental and embryonic experiences with predation risk affect prey offspring behaviour and performance. *Proc. R. Soc. B* **285**, 20180034. doi:10.1098/rspb.2018.0034

Donelan, S. C., Hellmann, J. K., Bell, A. M., Luttbeg, B., Orrock, J. L., Sheriff, M. J. and Sih, A. (2020). Transgenerational plasticity in human-altered environments. *Trends Ecol. Evol.* **35**, 115-124. doi:10.1016/j.tree.2019.09.003

Ehlers, B. K., Holmstrup, M., Schmidt, I. K., Sørensen, J. G. and Bataillon, T. (2018). Joint impact of competition, summer precipitation, and maternal effects on survival and reproduction in the perennial *Hieracium umbellatum*. *Evol. Ecol.* **32**, 529-545. doi:10.1007/s10682-018-9953-4

Engqvist, L. and Reinhold, K. (2016). Adaptive trans-generational phenotypic plasticity and the lack of an experimental control in reciprocal match/mismatch experiments. *Method. Ecol. Evol.* **7**, 1482-1488. doi:10.1111/2041-210X.12618

Ezard, T. H., Prizak, R. and Hoyle, R. B. (2014). The fitness costs of adaptation via phenotypic plasticity and maternal effects. *Funct. Ecol.* **28**, 693-701. doi:10.1111/1365-2435.12207

Fernández-González, M., Gonzalez-Barrientos, J., Carter, M. and Ramos-Jiliberto, R. (2011). Parent-to-offspring transfer of sublethal effects of copper exposure: Metabolic rate and life-history traits of Daphnia. *Rev. Chil. Hist. Nat.* **84**, 195-201. doi:10.4067/S0716-078X2011000200005

Fox, C., Waddell, K. and Mousseau, T. (1995). Parental host plant affects offspring life histories in a seed beetle. *Ecology* **76**, 402-411. doi:10.2307/1941199

Furness, A. I., Lee, K. and Reznick, D. N. (2015). Adaptation in a variable environment: Phenotypic plasticity and bet-hedging during egg diapause and hatching in an annual killifish. *Evolution* **69**, 1461-1475. doi:10.1111/evo.12669

Gagliano, M. and McCormick, M. I. (2007). Maternal condition influences phenotypic selection on offspring. *J. Anim. Ecol.* **76**, 174-182. doi:10.1111/j.1365-2656.2006.01187.x

Galloway, L. F. and Etterson, J. R. (2007). Transgenerational plasticity is adaptive in the wild. *Science* **318**, 1134-1136. doi:10.1126/science.1148766

Giordano, M., Groothuis, T. G. and Tschirren, B. (2014). Interactions between prenatal maternal effects and posthatching conditions in a wild bird population. *Behav. Ecol.* **25**, 1459-1466. doi:10.1093/beheco/aru149

Ghanizadeh Kazerouni, E., Franklin, C. E. and Seebacher, F. (2017). Parental exposure modulates the effects of UV-B on offspring in guppies. *Funct. Ecol.* **31**, 1082-1090. doi:10.1111/1365-2435.12817

Grafen, A. T. H. (1988). *On the Uses of Data on Lifetime Reproductive Success*. University of Chicago Press.

Grech, K., Maung, L. A. and Read, A. F. (2007). The effect of parental rearing conditions on offspring life history in *Anopheles stephensi*. *Malar. J.* **6**, 130. doi:10.1186/1475-2875-6-130

Gustafsson, S., Rengefors, K. and Hansson, L. (2005). Increased consumer fitness following transfer of toxin tolerance to offspring via maternal effects. *Ecology* **86**, 2561-2567. doi:10.1890/04-1710

Hafer, N., Ebil, S., Uller, T. and Pike, N. (2011). Transgenerational effects of food availability on age at maturity and reproductive output in an asexual collembolan species. *Biol. Lett.* **7**, 755-758. doi:10.1098/rsbl.2011.0139

Hayden, M. T., Holmes, K. D. and Arcila Hernández, L. M. (2021). Multigenerational consequences of aphid size on offspring phenotype and reproduction. *Entomol. Exp. Appl.* **169**, 947-958. doi:10.1111/eea.13086

Heckwolf, M. J., Meyer, B. S., Döring, T., Eizaguirre, C. and Reusch, T. B. (2018). Transgenerational plasticity and selection shape the adaptive potential of sticklebacks to salinity change. *Evol. Appl.* **11**, 1873-1885. doi:10.1111/eva.12688

Jablonka, E. and Raz, G. (2009). Transgenerational epigenetic inheritance: prevalence, mechanisms, and implications for the study of heredity and evolution. *Q. Rev. Biol.* **84**, 131-176. doi:10.1086/598822

Jacobs, B. S. and Lesmeister, S. A. (2012). Maternal environmental effects on fitness, fruit morphology and ballistic seed dispersal distance in an annual forb. *Funct. Ecol.* **26**, 588-597. doi:10.1111/j.1365-2435.2012.01964.x

Kozlowski, J. and Uchmanski, J. (1987). Optimal individual growth and reproduction in perennial species with indeterminate growth. *Evol. Ecol.* **1**, 214-231. doi:10.1007/BF02067552

Kozlowski, J. and Wiegert, R. G. (1987). Optimal age and size at maturity in annuals and perennials with determinate growth. *Evol. Ecol.* **1**, 231-244. doi:10.1007/BF02067553

Kuijper, B. and Hoyle, R. B. (2015). When to rely on maternal effects and when on phenotypic plasticity? *Evolution* **69**, 950-968. doi:10.1111/evo.12635

Kwok, K. W. H., Grist, E. P. M. and Leung, K. M. Y. (2009). Acclimation effect and fitness cost of copper resistance in the marine copepod *Tigriopus japonicus*. *Ecotoxicol. Environ. Saf.* **72**, 358-364. doi:10.1016/j.ecoenv.2008.03.014

Kyneb, A. and Toft, S. (2006). Effects of maternal diet quality on offspring performance in the rove beetle *Tachyporus hypnorum*. *Ecol. Entomol.* **31**, 322-330. doi:10.1111/j.1365-2311.2006.00775.x

Lack, D. (1954). The natural regulation of animal numbers. Oxford: Clarendon Press.

Latzel, V., Klimešová, J., Hájek, T., Gómez, S. and Šmilauer, P. (2010). Maternal effects alter progeny's response to disturbance and nutrients in two Plantago species. *Oikos* **119**, 1700-1710. doi:10.1111/j.1600-0706.2010.18737.x

Leicht, K. and Seppälä, O. (2019). Direct and transgenerational effects of an experimental heatwave on early life stages in a freshwater snail. *Freshw. Biol.* **64**, 2131-2140. doi:10.1111/fwb.13401

Leimar, O. and McNamara, J. M. (2015). The evolution of transgenerational integration of information in heterogeneous environments. *Am. Nat.* **185**, E55-E69. doi:10.1086/679575

Leips, J., Richardson, J. M., Rodd, F. H. and Travis, J. (2009). Adaptive maternal adjustments of offspring size in response to conspecific density in two populations of the least killifish, *Heterandria formosa*. *Evolution* **63**, 1341-1347. doi:10.1111/j.1558-5646.2009.00631.x

Lind, M. I., Zwoinska, M. K., Andersson, J., Carlsson, H., Krieg, T., Larva, T. and Maklakov, A. A. (2020). Environmental variation mediates the evolution of anticipatory parental effects. *Evol. Lett.* **4**, 371-381. doi:10.1002/evl3.177

Marshall, D. J. (2008). Transgenerational plasticity in the sea: context-dependent maternal effects across the life history. *Ecology* **89**, 418-427. doi:10.1890/07-0449.1

Marshall, D. and Uller, T. (2007). When is a maternal effect adaptive? *Oikos* **116**, 1957-1963. doi:10.1111/j.2007.0030-1299.16203.x

Matesanz, S., Ramos-Muñoz, M., Rubio Teso, M. L. and Iriondo, J. M. (2022). Effects of parental drought on offspring fitness vary among populations of a crop wild relative. *Proc. R. Soc. B* **289**, 20220065. doi:10.1098/rspb.2022.0065

Mayhew, P. J. (2001). Herbivore host choice and optimal bad motherhood. *Trends Ecol. Evol.* **16**, 165-167. doi:10.1016/S0169-5347(00)02099-1

Mbande, A., Tedder, M. and Chidawanyika, F. (2020). Offspring diet supersedes the transgenerational effects of parental diet in a specialist herbivore *Neolema abbreviata* under manipulated foliar nitrogen variability. *Insect Sci.* **27**, 361-374. doi:10.1111/1744-7917.12644

Mestre, L. and Bonte, D. (2012). Food stress during juvenile and maternal development shapes natal and breeding dispersal in a spider. *Behav. Ecol.* **23**, 759-764. doi:10.1093/beheco/ars024

Mikulski, A. and Pijanowska, J. (2017). The contribution of individual and maternal experience in shaping Daphnia life history. *Hydrobiologia* **788**, 55-63. doi:10.1007/s10750-016-2986-1

Mitchell, S. E. and Read, A. F. (2005). Poor maternal environment enhances offspring disease resistance in an invertebrate. *Proc. R. Soc. B* **272**, 2601-2607. doi:10.1098/rspb.2005.3253

Mojzes, A., Kalapos, T. and Kröel-Dulay, G. (2021). Drought in maternal environment boosts offspring performance in a subordinate annual grass. *Environ. Exp. Bot.* **187**, 104472. doi:10.1016/j.envexpbot.2021.104472

Monaghan, P. (2008). Early growth conditions, phenotypic development and environmental change. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 1635-1645. doi:10.1098/rstb.2007.0011

Moret, Y. (2006). "Trans-generational immune priming": specific enhancement of the antimicrobial immune response in the mealworm beetle, *Tenebrio molitor*. *Proc. R. Soc. B* **273**, 1399-1405. doi:10.1098/rspb.2006.3465

Mousseau, T. A. and Fox, C. W. (ed.) (1998). *Maternal Effects as Adaptations*. Oxford University Press.

Nystrand, M., Cassidy, E. J. and Dowling, D. K. (2016). Transgenerational plasticity following a dual pathogen and stress challenge in fruit flies. *BMC Evol. Biol.* **16**, 1-11. doi:10.1186/s12862-016-0737-6

Or, K. and Ward, D. (2007). Maternal effects on the life histories of bruchid beetles infesting *Acacia raddiana* in the Negev desert, Israel. *Entomol. Exp. Appl.* **122**, 165-170. doi:10.1111/j.1570-7458.2006.00509.x

Parker, T. H. (2002). Maternal condition, reproductive investment, and offspring sex ratio in captive red junglefowl (*Gallus gallus*). *The Auk* **119**, 840-845. doi:10.1642/0004-8038(2002)119[0840:MCRIAO]2.0.CO;2

Pías, B., Matesanz, S., Herrero, A., Gimeno, T. E., Escudero, A. and Valladares, F. (2010). Transgenerational effects of three global change drivers on an endemic Mediterranean plant. *Oikos* **119**, 1435-1444. doi:10.1111/j.1600-0706.2010.18232.x

Puy, J., de Bello, F., Dvořáková, H., Medina, N. G., Latzel, V. and Carmona, C. P. (2021). Competition–induced transgenerational plasticity influences competitive interactions and leaf decomposition of offspring. *New Phytol.* **229**, 3497-3507. doi:10.1111/nph.17037

Radersma, R., Hegg, A., Noble, D. W. and Uller, T. (2018). Timing of maternal exposure to toxic cyanobacteria and offspring fitness in *Daphnia magna*: Implications for the evolution of anticipatory maternal effects. *Ecol. Evol.* **8**, 12727-12736. doi:10.1002/ece3.4700

Raveh, S., Vogt, D. and Kölliker, M. (2016). Maternal programming of offspring in relation to food availability in an insect (*Forficula auricularia*). *Proc. R Soc. B* **283**, 20152936. doi:10.1098/rspb.2015.2936

Rotem, K., Agrawal, A. and Kott, L. (2003). Parental effects in *Pieris rapae* in response to variation in food quality: adaptive plasticity across generations? *Ecol. Entomol.* **28**, 211-218. doi:10.1046/j.1365-2311.2003.00507.x

Rowe, L. and Houle, D. (1996). The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc B* **263**, 1415-1421. doi:10.1098/rspb.1996.0207

Saastamoinen, M., Hirai, N. and van Nouhuys, S. (2013). Direct and trans-generational responses to food deprivation during development in the Glanville fritillary butterfly. *Oecologia* **171**, 93-104. doi:10.1007/s00442-012-2412-y

Salinas, S. and Munch, S. B. (2012). Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecol. Lett.* **15**, 159-163. doi:10.1111/j.1461-0248.2011.01721.x

Scheirs, J., Bruyn, L. D. and Verhagen, R. (2000). Optimization of adult performance determines host choice in a grass miner. *Proc. R. Soc. B* **267**, 2065-2069. doi:10.1098/rspb.2000.1250

Shama, L. N. (2015). Bet hedging in a warming ocean: predictability of maternal environment shapes offspring size variation in marine sticklebacks. *Glob. Change Biol.* **21**, 4387-4400. doi:10.1111/gcb.13041

Smith, C. C. and Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *Am. Natur.* **108**, 499-506.

Stearns, S. C. and Koella, J. C. (1986). The evolution of phenotypic plasticity in life–history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40**, 893-913.

Storm, J. J. and Lima, S. L. (2010). Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior. *Am. Nat.* **175**, 382-390. doi:10.1086/650443

Sultan, S. E., Barton, K. and Wilczek, A. M. (2009). Contrasting patterns of transgenerational plasticity in ecologically distinct congeners. *Ecology* **90**, 1831-1839. doi:10.1890/08-1064.1

Taborsky, B., Skubic, E. and Bruintjes, R. (2007). Mothers adjust egg size to helper number in a cooperatively breeding cichlid. *Behav. Ecol.* **18**, 652-657. doi:10.1093/beheco/arm026

Tariel, J., Luquet, É. and Plénet, S. (2020). Interactions between maternal, paternal, developmental, and immediate environmental effects on anti-predator behavior of the snail *Physa acuta*. *Front. Ecol. Evol.* **8**, 591074. doi:10.3389/fevo.2020.591074

Tufto, J. (2015). Genetic evolution, plasticity, and bet-hedging as adaptive responses to temporally autocorrelated fluctuating selection: A quantitative genetic model. *Evolution* **69**, 2034-2049. doi:10.1111/evo.12716

Uller, T., Nakagawa, S. and English, S. (2013). Weak evidence for anticipatory parental effects in plants and animals. *J. Evol. Biol.* **26**, 2161-2170. doi:10.1111/jeb.12212

Uller, T., English, S. and Pen, I. (2015). When is incomplete epigenetic resetting in germ cells favoured by natural selection? *Proc. R. Soc. B* **282**, 20150682. doi:10.1098/rspb.2015.0682

Van de Pol, M., Bruinzeel, L. W., Heg, D. I. K., Van Der Jeugd, H. P. and Verhulst, S. (2006). A silver spoon for a golden future: long–term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*). *J. Anim. Ecol.* **75**, 616-626. doi:10.1111/j.1365-2656.2006.01079.x

Vijendravarma, R. K., Narasimha, S. and Kawecki, T. J. (2010). Effects of parental larval diet on egg size and offspring traits in Drosophila. *Biol. Lett.* **6**, 238-241. doi:10.1098/rsbl.2009.0754

Vorburger, C., Gegenschatz, S. E., Ranieri, G. and Rodriguez, P. (2008). Limited scope for maternal effects in aphid defence against parasitoids. *Ecol. Entomol.* **33**, 189-196. doi:10.1111/j.1365-2311.2007.00949.x

Walsh, M. R., Cooley, F., Biles, K. and Munch, S. B. (2015). Predator-induced phenotypic plasticity within-and across-generations: a challenge for theory? *Proc. R. Soc. B* **282**, 20142205. doi:10.1098/rspb.2014.2205

Walsh, M. R., Castoe, T., Holmes, J., Packer, M., Biles, K., Walsh, M., Munch, S. B. and Post, D. M. (2016). Local adaptation in transgenerational responses to predators. *Proc. R. Soc. B* **283**, 20152271. doi:10.1098/rspb.2015.2271

Wang, Y., Li, S. R., Zeng, Z. G., Liang, L. and Du, W. G. (2017). Maternal food availability affects offspring performance and survival in a viviparous lizard. *Funct. Ecol.* **31**, 1950-1956. doi:10.1111/1365-2435.12903

Wang, Y., Li, S. R., Pei, M. Y., Wu, D. Y. and Du, W. G. (2021). Population origin, maternal effects, and hydric conditions during incubation determine embryonic and offspring survival in a desert-dwelling lizard. *Oecologia* **196**, 341-352. doi:10.1007/s00442-021-04932-9

Warner, D. A., Buckelew, A. M., Pearson, P. R. and Dhawan, A. (2015). The effect of prey availability on offspring survival depends on maternal food resources. *Biol. J. Linn. Soc.* **115**, 437-447. doi:10.1111/bij.12519

Waterman, R. and Sultan, S. E. (2021). Transgenerational effects of parent plant competition on offspring development in contrasting conditions. *Ecology* **102**, e03531.

Zehnder, C. and Hunter, M. (2007). A comparison of maternal effects and current environment on vital rates of *Aphis nerii*, the milkweed–oleander aphid. *Ecol. Entomol.* **32**, 172-180. doi:10.1111/j.1365-2311.2007.00853.x

Zhou, L. and Declerck, S. A. (2020). Maternal effects in zooplankton consumers are not only mediated by direct but also by indirect effects of phosphorus limitation. *Oikos* **129**, 766-774. doi:10.1111/oik.06898

Zirbel, K., Eastmond, B. and Alto, B. W. (2018). Parental and offspring larval diets interact to influence life-history traits and infection with dengue virus in *Aedes aegypti*. *R. Soc. Open Sci.* **5**, 180539. doi:10.1098/rsos.180539

Zizzari, Z. V., Van Straalen, N. M. and Ellers, J. (2016). Transgenerational effects of nutrition are different for sons and daughters. *J. Evol. Biol.* **29**, 1317-1327. doi:10.1111/jeb.12872