

What are parental condition-transfer effects and how can they be detected?

Russell Bonduriansky¹  | Angela J. Crean² 

¹Evolution & Ecology Research Centre and School of Biological, Earth and Environmental Sciences, University of New South Wales Australia, Sydney, NSW, Australia

²Animal Reproduction Group, School of Life and Environmental Sciences, Faculty of Veterinary Science, University of Sydney, Sydney, NSW, Australia

Correspondence

Russell Bonduriansky
Email: r.bonduriansky@unsw.edu.au

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Australian Research Council; Faculty of Veterinary Science, The University of Sydney

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Abstract

1. While it has been recognized for many years that parental condition can influence offspring performance, recent research on adaptive parental effects has focused primarily on anticipatory effects, whereby parents adjust the phenotype of their offspring for the anticipated environment. Here, we make the case that condition transfer is a widespread and important type of adaptive parental effect, and endeavour to clarify how such effects should be interpreted and studied.
2. Some authors have suggested that condition-transfer effects result simply from resource limitation constraints (passive condition transfer, or transmissive effects). However, condition transfer can also reflect evolved parental investment strategies (active condition-transfer effects). In some species, such strategies can involve cryptic mechanisms such as epigenetic inheritance.
3. As recently shown in this journal by Engqvist and Reinhold, condition-transfer effects can be obscured by anticipatory effects and interactions between the effects of parental and offspring environments. Nonetheless, we argue that these complications can be largely overcome by examining a broad range of ecologically relevant environments in both parental and offspring generations. This can be accomplished by adapting a powerful methodology from the nutritional sciences—the geometric framework—to research on parental effects.

KEYWORDS

adaptive, anticipatory, condition-dependence, epigenetic, maternal effect, nongenetic inheritance, parental effect, paternal effect, transgenerational

1 | INTRODUCTION

Nongenetic parental effects are now recognized as an important source of phenotypic variation and a key component of reproductive strategies in many species (Badyaev & Uller, 2009; Bonduriansky & Day, 2009; Danchin et al., 2011; Galloway & Etterson, 2007; Mousseau & Dingle, 1991; Mousseau & Fox, 1998; Roach & Wulff, 1987). In recent years, research attention has focussed on anticipatory parental effects, whereby parents predispose their offspring to do well in the anticipated environmental conditions. Other types of parental effects include “selfish” effects (where the quality of some or all offspring is reduced, releasing resources that can be used to increase

parental fecundity), “bet-hedging” effects (where a range of offspring phenotypes are produced, increasing the probability that at least some offspring will thrive in unpredictable environments) (Marshall & Uller, 2007), and the transfer of parental condition to offspring (“transmissive” or condition-transfer effects, Qvarnström & Price, 2001; Marshall & Uller, 2007; Crean & Bonduriansky, 2014), such that investment in offspring quality is positively correlated with parental condition.

Condition transfer effects have been categorized by some recent authors as non-adaptive, and we believe that these effects have been accorded less research attention than anticipatory effects. Here, we argue that condition transfer effects are often adaptive and, indeed, may be the most widespread type of adaptive parental effect. We also

outline approaches that can be used to detect such effects in empirical studies.

2 | WHAT ARE CONDITION TRANSFER EFFECTS?

Variation in condition is a major component of variation in phenotype and fitness within populations. “Condition” has been defined as an individual’s store of metabolic resources (Andersson, 1982; Rowe & Houle, 1996) or the efficiency of cellular processes (Hill, 2011), and incorporates genetic, epigenetic and environmental variation in phenotype (Bonduriansky et al., 2015; Hill, 2011). Individuals in high condition possess more metabolic resources, and are better able to convert those resources into fitness-enhancing traits, than individuals in low condition. Variation in condition can arise because individuals experience micro-environments that vary in resource abundance or stress levels, or as a result of variation in intrinsic factors such as health or age.

In addition to enhancing an individual’s own performance, condition is likely to influence parental investment (Qvarnström & Price, 2001), such that high-condition individuals typically provide more resources or better care to each individual offspring. Such effects have been observed in mammals (e.g. Fairbanks & McGuire, 1995), birds (e.g. Giordano, Groothuis, & Tschirren, 2014; Parker, 2002; Pooley, Kennedy, & Nager, 2014; Sasvari & Hegyi, 2001), fish (e.g. Gagliano & McCormick, 2007), insects (e.g. Bonduriansky & Head, 2007; Wong & Kölliker, 2012), echinoderms (Caballes, Pratchett, Kerr, & Rivera-Posada, 2016), and other taxa (Mousseau & Fox, 1998). Obvious forms of parental investment are limited to females in most species: for example, females allocate nutrients to the production of yolk and/or to the nourishment of embryos or neonates. However, paternal care occurs in some fish, amphibians, birds, mammals and insects (Klug, Bonsall, & Alonzo, 2013; Kokko & Jennions, 2008), and paternal allocation of resources to offspring often varies with paternal condition (Badyaev & Hill, 2002; Hunt & Simmons, 2000). Likewise, genetic variation in parental condition can affect offspring performance non-genetically via indirect genetic effects, whereby alleles expressed in the parent affect offspring development (Head, Berry, Royle, & Moore, 2012; Wolf, Brodie, Cheverud, Moore, & Wade, 1998; Wolf, Moore, & Brodie, 1997).

Condition-transfer effects are widely recognized in species that exhibit conventional forms of parental investment, such as nutrient provisioning (in which these effects are sometimes called “silver spoon effects”). However, recent evidence suggests that condition-transfer is widespread even in species lacking conventional forms of parental investment (for which the term “silver spoon effects” seems less appropriate). In such cases, condition-transfer effects can be mediated by a variety of nongenetic parental effects that do not involve nutrient transfer or other conventional forms of parental care (Crean & Bonduriansky, 2014; Curley, Mashoodh, & Champagne, 2011; Rando, 2012; Rodgers, Morgan, Bronson, Revello, & Bale, 2013; Soubry, Hoyo, Jirtle, & Murphy, 2014; Zajitschek, Zajitschek, & Manier, 2017). For

example, paternal effects can be mediated by sperm-borne epigenetic factors (e.g. DNA methylation patterns), or by RNA, proteins or other molecules transferred in the seminal fluid (Eaton et al., 2015), and recent evidence has revealed paternal effects in species where males transfer small ejaculates and provide no care for their offspring (Crean, Adler, & Bonduriansky, 2016). In such cases, high-condition males can produce high-condition offspring, just as in species with conventional forms of paternal investment. For example, in the neriid fly *Telostylinus angusticollis*, males reared on a nutrient-rich larval diet produce larger offspring than males reared on a nutrient-poor larval diet (Adler & Bonduriansky, 2013; Bonduriansky & Head, 2007; Bonduriansky, Runagall-McNaull, & Crean, 2016; Crean, Kopps, & Bonduriansky, 2014). In such cases, high condition may enable parents to transfer advantageous epigenetic variants to their offspring, and the condition-dependence of such effects may be maintained by (as yet unknown) costs of developing, maintaining, or deploying the required epigenetic machinery. For example, just as the maintenance of genome-wide DNA methylation states is strongly age-dependent, with deleterious changes accompanying (and perhaps causing) senescence (“epigenetic clock”: Horvath, 2013), stress may accelerate the clock (Horvath et al., 2016; Simons et al., 2016; Zannas et al., 2015), and some of these epigenetic changes may be transmissible to offspring (Skinner, 2015; Wang, Liu, & Sun, 2017). The taxonomic distribution, proximate basis, and ecological role of condition-transfer effects in such non-resource systems remain poorly understood.

3 | CONDITION TRANSFER IS AN ADAPTIVE PARENTAL EFFECT

Parental effects are classified as adaptive when they increase the lifetime reproductive success of the parent (Marshall & Uller, 2007). We argue that condition transfer effects are often adaptive because the transfer of high parental condition to offspring will tend to enhance offspring performance. Unless such effects are subject to strong trade-offs with other functions, such effects can thereby increase the fitness of high-condition parents. Importantly, condition transfer effects can be adaptive even if low-condition parents transfer their low-condition via the transmission of pathology, toxins or effects of advanced parental age (e.g. see O’Dea, Noble, Johnson, Hasselson, & Nakagawa, 2016). Such effects can reduce the fitness of both low-condition parents and their offspring. However, because high-condition individuals typically produce more offspring than low-condition individuals, any trait that enhances the fitness of high-condition individuals will tend to be advantageous on average. In other words, net selection is expected to favour condition transfer effects for the same reason that net selection favours other condition-dependent traits, such as sexual signals (Rowe & Houle, 1996): even though low-condition individuals are likely to lose fitness by signalling their low condition, such traits are still under positive net selection (and are considered adaptive) because they increase fitness of high-condition individuals, and therefore tend to enhance fitness on average. Similarly, because the fitness advantage to high-condition individuals outweighs the fitness

disadvantage to low-condition individuals, condition transfer effects will tend to be under positive net selection.

Notably, condition transfer effects are likely to occur to some extent as unavoidable side-effects of variation in parental condition on the development of gametes, embryos or juveniles. All costly traits are expected to exhibit condition-dependent expression, and reproductive traits typically exhibit particularly strong condition dependence (Andersson, 1982; Rowe & Houle, 1996). Consequently, many nongenetic factors transmitted to offspring (such as epigenetic factors associated with maternal and paternal DNA, proteins and RNA in the egg cytoplasm, maternal reproductive behaviour and oviposition site choice, or intra-uterine factors) will be condition-dependent, resulting in some degree of condition transfer. When parental condition is affected by environmental factors such as diet or stress, and parents transmit these effects to their offspring, the resulting condition-transfer effects fit Marshall and Uller's (2007) definition of "transmissive effects," which they classified as nonadaptive. However, we suggest that, for the reasons outlined above, transmission of environmentally induced condition is likely to be under positive net selection, although the effects of such passive condition-transfer on fitness could be weak.

When selection favours increased parental investment in offspring quality, such pre-existing condition-transfer effects can be elaborated into more complex strategies of condition-dependent maternal or paternal investment (active condition-transfer effects). Nevertheless, the evolution of condition transfer effects (as well as anticipatory effects) will be subject to the same constraints as the evolution of other forms of parental investment. Parental effects that enhance offspring quality are expected to benefit the parents as well. However, if such effects are costly for parents, the evolution of such effects will be limited by trade-offs with other fitness-enhancing functions, such as offspring number (Smith & Fretwell, 1974). Indeed, it is possible for high-condition females to benefit by producing offspring of lower quality (e.g. see Senior, Lim, Adolfsson, Lamatsch, & Nakagawa, 2016). These conditions tend to be more restrictive for males because uncertainty of paternity and the risk of cuckoldry will select against costly investment in offspring quality (Wickler, 1985). For example, seminal fluid-borne factors can influence offspring sired by other males (Crean et al., 2014), so paternal condition transfer effects via the seminal fluid may be subject to cuckoldry (Crean et al., 2016). In contrast, paternal effects mediated by sperm-borne epigenetic factors such as DNA methylation marks are tightly associated with fertilization and therefore free of the risk of cuckoldry (Bonduriansky & Day, 2013). Sperm-borne epigenetic variation may therefore represent a common mechanism for adaptive paternal effects. Indeed, the male germ line appears to be highly sensitive to epigenetic reprogramming by a variety of environmental factors (Curley et al., 2011; Pembrey, Saffery, Bygren, & Epidemiology N.i.E., 2014; Soubry et al., 2014).

The relation between parental condition and the quantity or quality of condition-dependent factors (such as nutrients or epigenetic factors) that are transmitted to offspring could take a variety of forms. In the simplest case, this relationship could be linear, but more complex, nonlinear patterns are likely to occur in many species. For example, low-condition parents might disproportionately reduce investment

per offspring to conserve resources, or, alternatively, investment per offspring could level off at high levels of parental condition because of diminishing returns on increased investment. In such nonlinear cases, condition-transfer can be "selfish" by Marshall and Uller's (2007) definition, at least over part of the range of parental condition.

4 | CONDITION TRANSFER EFFECTS ARE LIKELY TO BE WIDESPREAD

The pre-conditions for the evolution of condition transfer effects appear to be less restrictive than the pre-conditions for the evolution of other types of adaptive parental effects. A key requirement for the evolution of anticipatory parental effects is environmental predictability across generations. When current environmental conditions are positively correlated with environmental conditions in the following generation, parents should adjust offspring phenotype for the same conditions that the parents themselves experienced (Crean, Dwyer, & Marshall, 2013). Conversely, when environmental conditions fluctuate predictably across generations between two environmental states, parents should optimize the phenotype of their offspring for the alternative environmental state to the one that the parents themselves experienced (Dey, Proulx, & Teotonio, 2016). A further requirement is the evolution of a complex machinery for assessing environmental conditions and adjusting offspring phenotype accordingly. Moreover, offspring that end up in the "wrong" environment may pay a substantial fitness cost (Marshall, 2008), and the risk of such mismatch between the anticipated and actual environment will tend to select against anticipatory effects. Theory suggests that the range of environmental predictability that favours the evolution of bet-hedging parental effects is even narrower than that for anticipatory effects (Proulx & Teotonio, 2017).

By contrast, the evolution of condition transfer effects is not contingent on environmental predictability because high condition is likely to enhance offspring fitness in any environment. Such effects also do not depend on the evolution of complex cellular, physiological or neural mechanisms for assessing environmental conditions and adjusting offspring phenotype accordingly. Instead, condition transfer simply involves condition-dependent investment in gametes or offspring and, as we have noted above, some degree of condition transfer is likely to occur even in the absence of selection for increased parental investment. When selection favours increased investment per offspring, such condition-dependent reproductive traits can be readily elaborated into more complex parental investment strategies. These considerations suggest that condition transfer may be the most widespread type of adaptive parental effect.

5 | INVESTIGATING CONDITION TRANSFER EFFECTS

Nongenetic parental effects occur when parents influence their offspring, but parent-offspring phenotypic covariance does not result from the transmission of alleles from parents to their offspring (Wolf

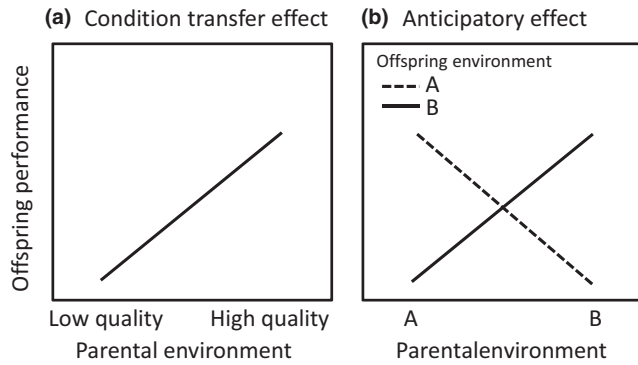


FIGURE 1 In the absence of complicating factors (see text and Figure 2), condition transfer effects can be detected as a positive effect of parental condition on offspring performance (a), while anticipatory effects can be detected as an interaction between parental environment and offspring environment on offspring performance (b)

& Wade, 2009). To test for nongenetic condition transfer effects, it is therefore necessary to manipulate parental phenotypic condition while controlling for genotype, and quantify effects on offspring performance. For example, parents can be randomly assigned to diets of varying quality (Bonduriansky & Head, 2007), social or sensory environments that induce varying levels of stress (Sheriff, Krebs, & Boonstra, 2009), or inbred to varying degrees while controlling for genotype (Fox & Reed, 2011). Manipulated (focal) individuals can then be crossed in a fully factorial design (allowing for detection of interactions between maternal and paternal effects), or, alternatively, paired with mates reared under standardized conditions (Bonduriansky, Crean, & Day, 2012). Under condition-transfer effects, a positive association between parental condition and offspring

performance is predicted (although other factors can complicate interpretation of such patterns: see below). In contrast, to detect anticipatory effects, both parental and offspring environments must be manipulated (match/mismatch experiments) and, in the absence of complicating factors (see below), the observation that offspring performance is enhanced in the environment that is predicted by parental environment will provide evidence of an anticipatory effect (Figure 1). Nonetheless, Engqvist and Reinhold (2016) have highlighted a number of factors that can complicate the detection of both anticipatory and condition transfer effects. While they have suggested potential strategies for the study of anticipatory effects, we will focus here on strategies for the study of condition transfer effects.

First, Engqvist and Reinhold have noted that the experimental inference can be complicated when condition transfer and anticipatory effects co-occur. For example, if resource-limited (low-condition) parents predispose their offspring to perform better under conditions of resource limitation, then it is possible that offspring of low-condition parents would perform better than offspring of high-condition parents when offspring environment is resource-poor (Figure 2a). Second, Engqvist and Reinhold (2016) noted that experimental inference can be complicated by interaction between offspring and parental environments, and the fact that such interactions can have nonlinear effects (as illustrated in their Figure 2). For example, the offspring of high-condition parents may enjoy a considerable performance advantage in a moderately resource-limited environment, but might not exhibit an appreciable performance advantage in a very harsh or very favourable environment (Figure 2b). This means that, depending on the particular parental and offspring environments chosen for study, the estimated magnitude of the condition transfer effect can be zero, small or large, and the interaction between the

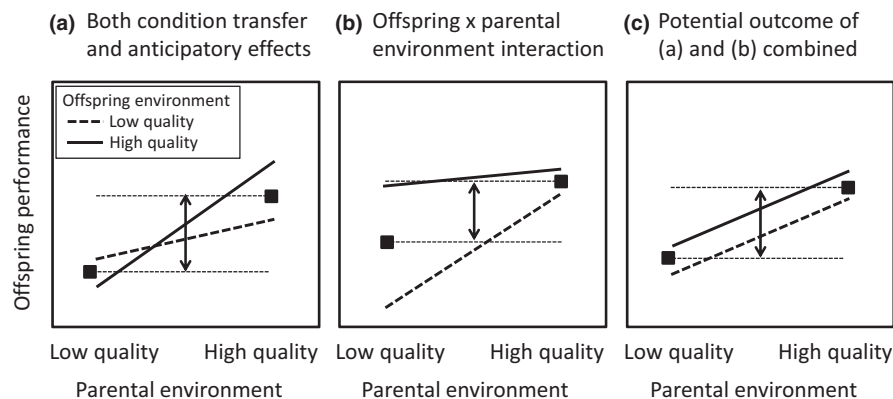


FIGURE 2 The detection of condition transfer effects can be complicated in some situations: (a) Condition transfer can co-occur with anticipatory effects, and this can enhance relative performance of offspring of poor-condition parents in a resource-limited environment. (b) Parental condition and offspring condition can interact: for example, offspring of high-condition parents can have a greater advantage when they are resource-limited. (c) Both types of complications could also occur at the same time: for example, anticipatory effects can enhance the performance of offspring of poor-condition parents in a resource-limited environment, while an interaction between parental and offspring condition can reduce the advantage of offspring of high-condition parents in a resource-rich environment. Such complications can affect the estimated magnitude of condition transfer effects in each offspring environment, or even obscure the effect entirely in one environment. However, in all these cases condition transfer should still be detectable as a positive main effect (vertical arrow) of parental condition when offspring performance is assessed in both environments, reflecting the difference in mean performance (closed points) between offspring of low- and high-condition parents

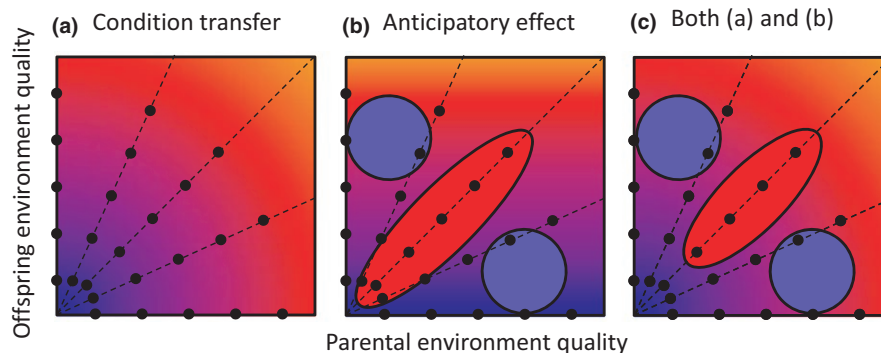


FIGURE 3 Using the geometric framework, both parental and offspring environments can be manipulated simultaneously, generating several treatment combinations (closed points), and the effect on offspring performance can be represented as a nonlinear response surface (depicted as a colour gradient, with blue denoting low values and red denoting high values of offspring performance). (a) Using this design, a condition-transfer effect can be detected as a positive effect of parental environment quality (condition), reflected in a response surface that rises to the right. Combined with the positive effect of offspring environment, this will result in a surface that rises away from the origin. (b) An anticipatory effect can be detected as a ridge of increased offspring performance along the diagonal (represented by the red ellipse) and areas of reduced offspring performance in areas of mismatch (represented by the blue circles). Because increasing offspring environment quality will have a positive overall effect on offspring performance, the areas of increased/decreased offspring performance corresponding to the anticipatory effect will appear as ridges and troughs on a surface that rises towards the top. (c) Likewise, a combination of anticipatory and condition-transfer effects can be detected as ridges and troughs on a surface that rises away from the origin

parental and offspring environment on the magnitude of this effect can be positive or negative. Of course, both types of complications can occur in some systems, and experimental results may reflect a combination of these effects (Figure 2c).

Yet, despite the complications highlighted by Engqvist and Reinhold, we believe that the detection of condition-transfer effects is relatively straight-forward: these complications can be overcome by manipulating both parental and offspring environments and, ideally, by examining a broad range of ecologically relevant environments in both parental and offspring generations. As Engqvist and Reinhold point out, a condition transfer effect should enhance the relative performance of offspring of high-condition parents in any environment. Although a strong anticipatory effect could counteract this effect and allow the offspring of low-condition parents to outperform the offspring of high-condition parents under certain conditions, measurement of offspring performance across both parental environments (or, better yet, across several ecologically relevant environments) should nonetheless reveal a net advantage for offspring of high-condition parents. Statistically, a condition transfer effect should therefore be reflected in a positive main effect of parental condition on offspring performance. Of course, detection of such effects will not provide a complete understanding of the roles of different types of parental effects. As noted by Engqvist and Reinhold, gauging the precise contributions of different types of parental effects to offspring performance is probably not possible without understanding the proximate mechanisms involved in each type of effect, and manipulating the factors involved. Nonetheless, assessing offspring performance across multiple environments will make it possible to detect condition transfer effects (as well as anticipatory effects), and to determine how the estimated magnitudes of these effects vary with parental and offspring environment. Obtaining such estimates is an essential first step in research on parental effects.

While investigating effects of parental environment across two offspring environments can overcome some of the pitfalls of using a single offspring environment, additional insights can be gleaned from experiments that investigate more than two environments. Condition transfer can be regarded as an example of transgenerational plasticity, whereby a given parental genotype alters its investment in reproduction depending on the availability of metabolic resources. In studies of within-generation plasticity, examining multiple environments makes it possible to detect nonlinear effects, and therefore reduces the risk of misinterpretation that can occur when just two environments are examined (Rocha & Klaczko, 2012). We suggest that, for similar reasons, studies of parental effects should aim to examine multiple environmental states that span an ecologically relevant gradient. A particularly powerful paradigm for the study of environmental effects on performance and development is the geometric framework (Simpson & Raubenheimer, 2012). In nutritional geometry studies, two environmental factors (nutrients) are manipulated simultaneously, with each environmental factor spanning a broad range of values, typically resulting in 20–30 different environmental (diet) treatment combinations. This makes it possible to detect nonlinear effects and complex interactions, reflected in a response surface for the trait of interest.

The geometric framework can be adapted for research on effects of parental environment on offspring (Bonduriansky et al., 2016). For example, parental condition can be manipulated simultaneously with offspring environment quality, providing a detailed picture of how parental condition-transfer effects interact with offspring condition. This approach can make it possible to detect condition-transfer effects, anticipatory effects, and combinations of both types of effects (Figure 3). The geometric approach could therefore provide valuable insights and reduce the risk of misinterpretation in research on parental effects, just as it has in the nutritional sciences.

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AUTHORS' CONTRIBUTIONS

R.B. and A.J.C. conceived the ideas and wrote the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

This study does not use any data.

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