

COMMENTARY

Adaptive trans-generational phenotypic plasticity and the lack of an experimental control in reciprocal match/mismatch experiments

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Summary

1. Parental information about the prevailing environmental condition may enable offspring to adjust their phenotypes in accordance with future demands.
2. The state-of-the-art experimental test of the occurrence of such adaptive trans-generational phenotypic plasticity is a ‘match/mismatch’ approach: a fully factorial reciprocal transplant experiment where offspring encounter environments either matching or mismatching parents’ experience.
3. Here, we highlight that a hidden assumption of this approach is that the effect of early and late offspring environment acts completely additively on offspring fitness. Likely violations of this assumption, such that early ‘silver-spoon’ effects are more valuable when later environmental conditions are relatively harsh, will bias the estimates of potential trans-generational effects.
4. We discuss the different implications of this on the interpretation of the outcome of match/mismatch experiments and suggest different complementary and alternative approaches.

Key-words: anticipatory parental effects, experimental design, parental programming, predictive response, silver-spoon, statistical interactions

Introduction

Organisms often face variable environments implying that different phenotypic attributes may be advantageous depending on the prevailing ecological condition. Thus, natural selection may often favour a plastic response to current conditions rather than a fixed static strategy (West-Eberhard 1989; van Tienderen 1997; Nylin & Gotthard 1998). Examples of such adaptive phenotypic plasticity are numerous and come from various taxa in response to many different environmental stimuli (see, e.g. Dudley & Schmitt 1996; Agrawal 1998, 2001; Frost 1999; Weisser, Braendle & Minoretti 1999; Pfennig & Murphy 2000; DeWitt & Scheiner 2004). Arguably the most prominent and illustrative evidence comes from phenotypic plasticity in response to a changing risk of predation (see, e.g. Appleton & Palmer 1988; Brönmark & Miner 1992; Tollrian 1995; Weisser, Braendle & Minoretti 1999; Relyea 2001; Frommen *et al.* 2011; Stratmann & Taborsky 2014).

If organisms face very different environmental regimes, this may demand quite substantial phenotypic modifications (Jacarini *et al.* 1983; Schmid-Hempel 1992; Agrawal, Laforsch & Tollrian 1999). Nevertheless, gaining information about the environment during an organism’s own lifetime only enables

relatively late developmental adjustments. It should therefore be advantageous to have reliable information as early as possible enabling an unconstrained development along an optimal trajectory. Often, the parental environment is predictive of the environment likely to be faced by their offspring. If this is the case, trans-generational cues would provide an effective channel in which offspring could potentially receive adequate information very early in their development (Mousseau & Dingle 1991; Mousseau & Fox 1998; Fox *et al.* 1999; Kuijper & Hoyle 2015) and as a consequence could modify their phenotype adaptively according to the provided parental information (Fox, Thakar & Mousseau 1997; Agrawal, Laforsch & Tollrian 1999; Bateson *et al.* 2004; Gustafsson, Rengefors & Hansson 2005; Moret 2006; Cleal *et al.* 2007; Galloway & Etlerson 2007; Marshall 2008; Hasselquist & Nilsson 2009; Sultan, Barton & Wilczek 2009; Latzel *et al.* 2014; Shama *et al.* 2014; Stratmann & Taborsky 2014). There are many different names used in the literature to describe such parentally mediated adaptive plasticity (Uller, Nakagawa & English 2013). Nevertheless, the terms ‘adaptive trans-generational plasticity’ (e.g. Mousseau & Fox 1998; Galloway & Etlerson 2007), ‘anticipatory parental effects’ (Marshall & Uller 2007; Uller, Nakagawa & English 2013), ‘adaptive parental programming’ (e.g. Horton & Stetson 1990; Reddon 2012; Raveh, Vogt & Kölliker 2016) and ‘predictive adaptive response’ (Gluckman, Hanson & Spencer 2005; Cleal *et al.* 2007) highlight how selection may

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form parental effects to enable offspring to develop optimally in their prospective environment. The different names also imply that the phenomenon can be separated in three essential ingredients. First, it has to be established that there is a parental cue, which is environment-dependent. Secondly, there needs to be phenotypic offspring plasticity in response to this cue. Finally, the whole signal–response complex should be adaptive, that is result in positive effects on genotypic fitness. Experimentally demonstrating such adaptive trans-generational plasticity has proven challenging (cf. Marshall & Uller 2007; Nettle & Bateson 2015). Yet, although each one of these elements is likely to have its own share of complications, the major focus of this contribution is to highlight the difficulties to explicitly pinpoint the effects on fitness, especially the problem of disentangling anticipatory parental fitness effects from other parental effects affecting offspring fitness (i.e. ‘silver-spoon’ effects). These cannot be ascribed to an adaptive match of offspring phenotype to the environment and therefore are usually not considered to constitute adaptive trans-generational plasticity (cf. Uller, Nakagawa & English 2013; Krause & Naguib 2014; Nettle & Bateson 2015; Raveh, Vogt & Kölliker 2016). Indeed, a recent meta-analysis established only weak overall evidence for fitness-associated anticipatory parental effects (Uller, Nakagawa & English 2013), yet we caution here that this may partly be due to methodical constraints linked to the match/mismatch approach rather than reflecting true effect sizes.

Identifying anticipatory parental effects by the match/mismatch approach

Indicative of adaptive trans-generational plasticity are offspring fitness benefits from growing up in the same environment as the parents experienced. Thus, if there are two, otherwise fitness equivalent, environments *A* and *B*, we expect an offspring whose parents experienced environment *A* to have higher fitness in *A* than in *B* and vice versa (see Fig. 1a). In line with these arguments, an often recommended and frequently adopted design to test for adaptive trans-generational plasticity is a reciprocal transplant or match/mismatch experiment (Gotthard & Nylin 1995; Doughty & Reznick 2004; Marshall & Uller 2007; Uller, Nakagawa & English 2013; Groothuis & Taborsky 2015). In principle, this is a fully factorial design consisting of at least two parental environments (providing cues) and corresponding offspring environments. Offspring are subsequently translocated among alternative environments that are either matching or mismatching their previous experience. Such a reciprocal transplant experiment has often been used to test for reversals in phenotypic optima and thus adaptive phenotypic plasticity (e.g. Shapiro 1976; Trussell 2000; Lorenzon, Clobert & Massot 2001; Yeap, Black & Johnson 2001; Shama *et al.* 2014).

However, we are confronted with a first problem because not all environments are equally suitable for offspring development and survival. In the following, we denote *B* as a relatively poor environment and *A* as a comparatively good environment. Now, it is well possible that offspring are not always

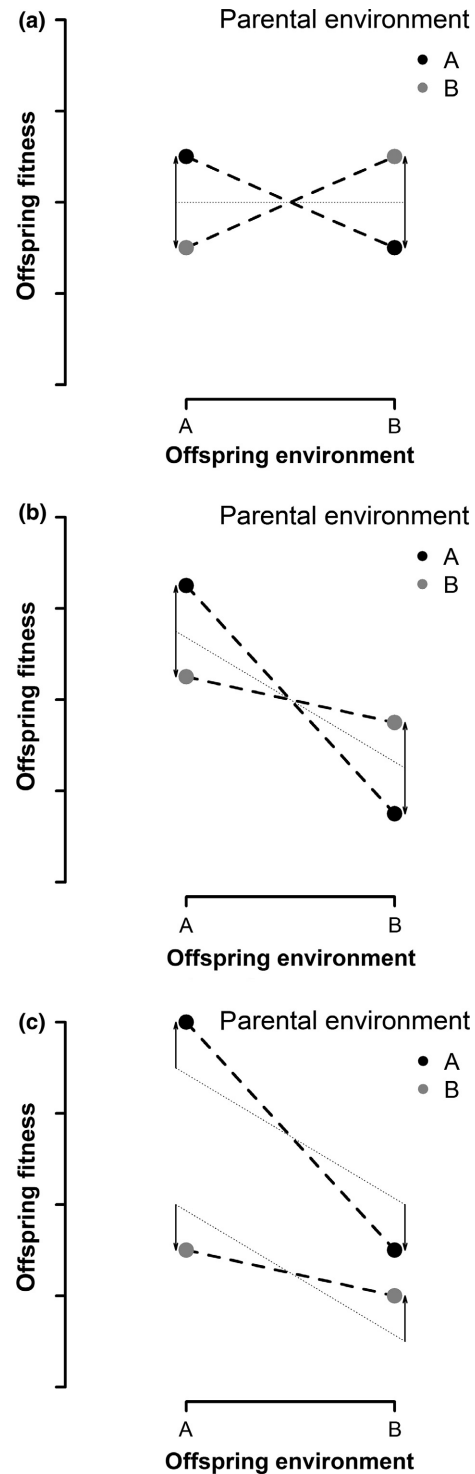


Fig. 1. Schematic illustrations of three different outcomes all consistent with footprints of trans-generationally induced adaptive phenotypic plasticity. The dotted lines indicate expectations without anticipatory parental effects. The arrows indicate changes to this due to the match or mismatch of parent–offspring environments, and the dots represent the actual measured effects. In (a), environments *A* and *B* are equivalent regarding offspring reproductive potential. In (b), the two environments differ in absolute quality and offspring have overall higher reproductive potential in environment *A*. In (c), there is an additional ‘silver-spoon’ effect, and offspring are generally doing better if they are born by parents from environment *A*.

performing best in a parentally matched environment – an offspring growing up in *A* may well do better than in *B* although its parents experienced *B* (e.g. Dudley & Schmitt 1996; Galloway & Etterson 2007). Indeed, the evidence of immediate environmental effects on offspring fitness is overwhelming (see, e.g. Boggs & Ross 1993; Engqvist & Sauer 2003; Gustafsson, Rengefors & Hansson 2005; Bonduriansky & Head 2007; Sultan, Barton & Wilczek 2009; Uller, Nakagawa & English 2013; Krause & Naguib 2014). Yet, crucial for the idea of adaptive trans-generationally mediated plasticity in these situations is simply that in each offspring environment, those individuals are doing best whose parents experienced the same environment. This is most easily conceptualized by crossing fitness reaction norms (see Fig. 1b). Nevertheless, even this simple principle may be violated if we additionally assume that depending on the quality of the parental environment, parents are differently able to provide parental benefits, whose effects are expressed independent of offspring environment. For instance, parents from high-quality habitats may produce larger eggs or provide their offspring with more valuable resources (Kaplan 1987; Roach & Wulff 1987; Rossiter, Cox-Foster & Briggs 1993; Bertram & Strathmann 1998; Christians 2002; Bonduriansky & Head 2007). In this case, the parental environment will itself shape the quality of the early environment faced by the developing offspring. Thus, parents from *A* may enable their offspring a head start in life, irrespective of whether these later grow up in *A* or *B*. Such ‘silver-spoon’ effects (or ‘carry-over’ effects, cf. Uller, Nakagawa & English 2013), that is individuals born in good conditions have fitness advantages later in life (see Monaghan 2008), are actually very well documented (Lindström 1999; Fox & Czesak 2000; Qvarnström & Price 2001; Taborsky 2006; Van de Pol *et al.* 2006; Nussey *et al.* 2007; Krist 2011; Segers & Taborsky 2011; Franzke & Reinhold 2013; Hopwood, Moore & Royle 2014). Although offspring phenotypic adjustment due to ‘silver-spoon’ effects is certainly a trans-generational effect, it does not represent adaptive plasticity as parent experiences, such as food and resource limitation, simply carry over to the next generation and constrain offspring growth, survival and/or reproductive success (Uller, Nakagawa & English 2013; Nettle & Bateson 2015; Raveh, Vogt & Kölliker 2016). With substantial ‘silver-spoon’ effects, it is well possible that, in absolute terms, offspring developing in *B* are doing better with parents from *A* than with parents from *B*. Thus, the ‘silver-spoon’ may seem to override any beneficial effects due to parent–offspring environmental matching enabling anticipatory effects. Yet, this is only superficially so. In this scenario, offspring may still be doing *relatively* better if they grow up in the same environment as their parents experienced (see Fig. 1c). Thus, the only possible conclusive diagnosis of adaptive trans-generational plasticity from such a match/mismatch approach is a parental environment \times offspring environment interaction. More specifically, this needs to be a *positive* interaction as we would demand $\hat{w}_{AA} + \hat{w}_{BB} - (\hat{w}_{AB} + \hat{w}_{BA}) > 0$. Here, \hat{w}_{ij} represents fitness (or proxy thereof) of an offspring having parents from environment *i*, yet themselves growing up in environment *j*. From this, one can see that the interaction term here is fully equivalent

with a factor ‘matched vs. mismatched’ environments controlling for offspring environmental and paternal environmental (‘silver-spoon’) effects on fitness.

Outlining the problem

As seen in the previous section, using a reciprocal match/mismatch approach to infer adaptive trans-generational plasticity is not as straightforward as on first sight (see also Uller, Nakagawa & English 2013; Krause & Naguib 2014). Most importantly, all resulting patterns including a positive interaction term describing parental–offspring environmental matching are consistent with adaptive parental programming of offspring (see Fig. 1). Note that this makes any statistical inferences sensitive to data transformation (e.g. log-transformation due to non-Gaussian distribution) as this will change the magnitude of the interaction term (see, e.g. Stanton & Thiede 2005). However, another problematic issue that we want to highlight here is that such parental environment \times offspring environment interactions can easily be caused by many other processes, and thus, adaptive trans-generational plasticity needs not be involved if such interaction effects are found. In other words, a match/mismatch experiment lacks an experimental control (we will return and discuss an appropriate control later on). In principle, a match/mismatch approach indirectly assumes that early environmental (i.e. parental) and later environmental effects acts completely additively on offspring fitness. Yet, this is not an inherent premise of hypotheses concerning anticipatory trans-generational effects. Thus, the assumptions of the experiment do not match the underlying assumptions of the hypothesis (see also Nettle & Bateson 2015).

We can think of several scenarios causing non-additively acting environmental effects. Arguably, the most likely (at least conceptually most illustrating) situation is that parental/early environment effects are more or less important depending on the harshness of later adult conditions (see, e.g. Semlitsch & Gibbons 1990; Dziminski & Roberts 2006; Krist & Muncinger 2015). Positive parental effects may be crucial if an individual later on is facing poor conditions, but they may affect survival and reproductive success to a lesser degree if adult conditions are very favourable (cf. Fig. 2). For instance, the positive effect of egg size indicative of maternal nutritional provision is often more pronounced in stressful environments (e.g. Fox 2000; Dziminski & Roberts 2006; Krist & Muncinger 2015). We will refer to this kind of early \times late synergistic environmental effects as being caused by ‘beneficially saturated’ conditions – individuals experiencing beneficial conditions either early or late will be doing almost equally well as individuals facing benign conditions throughout, and only offspring confronted with permanent harsh conditions will be handicapped. Another possibility is that the early \times late environmental interaction effects are ‘detrimentally saturated’. Here, only offspring facing relatively good conditions both during early and later life will be favoured; poor conditions either early or later in development will both have detrimental effects, yet the combined effect is weak (cf. Fig. 2). Hence, the detrimental effects

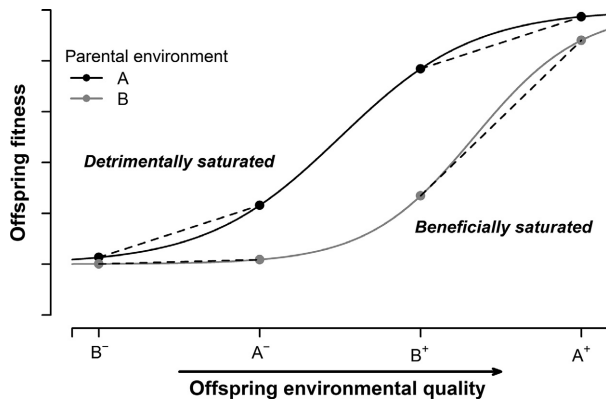


Fig. 2. Hypothetical example illustrating the concept of detrimentally and beneficially saturated environments. Conditions *A* and *B* represent relatively favourable and harsh conditions, respectively. The left-hand side illustrates a potential outcome (dots and dashed lines) from a match/mismatch experiment performed at the lower end of the spectrum of environmental quality (B^- vs. A^-), where ‘silver-spoon’ effects possibly only make a difference if offspring are facing tolerable environmental conditions (A^-). In contrast, the right-hand side illustrates the corresponding pattern under relatively rich conditions. Then, the ‘silver-spoon’ may have less impact if offspring are facing extremely favourable conditions (A^+) later in life.

of the poor environmental conditions are saturated, and positive parental effects are expected to be most pronounced if they later experience benign conditions (see, e.g. Semlitsch & Gibbons 1990; Krist 2011). We do not suggest here that beneficial or detrimental environmental saturation necessarily represent fixed system properties. Instead, it seems plausible that both phenomena can be observed in any system and rather represent points in a continuum, where detrimental environmental saturation is a leading feature in the low range of environmental quality distribution, whereas beneficial saturation is dominating in the high range (cf. Fig. 2).

What is important here is that we do not necessarily have to consider any anticipatory parental effects to explain why offspring are doing relatively better or worse if they experience the same or different environments as their parents; there are other mechanisms that may cause this apparent statistical parental environment \times offspring environment interaction. We must recall, however, that the interaction is the only possible positive diagnosis of an anticipatory parental effect from a match/mismatch experiment. Thus, the different mechanisms are confounded in this particular experimental design.

Now let us have a look at how beneficially saturated and detrimentally saturated environmental effects may affect our conclusions regarding parental programming. In the beneficially saturated scenario, the statistical interaction effect will have a *negative* value and offspring experiencing matched environments will evidently do relatively worse than offspring from mismatched environments (cf. Fig. 2). Thus, any positive parental environment \times offspring environment statistical interaction generated by anticipatory parental effects will be offset by this negative effect. In other words, beneficially saturated environmental effects will act to conceal any potential signatures of adaptive trans-generational phenotypic plasticity. Yet, this

does not necessarily mean that trans-generational effects are absent. Thus, in principle, it is possible that offspring are doing relatively poorer in matched parent/offspring environments although they receive information that is translated into beneficial effects (Fig. 3a). If environmental effects are detrimentally saturated, on the other hand, offspring experiencing matched environments will do relatively better than offspring from mismatched environments (cf. Fig. 2). Thus, detrimentally saturated environmental effects will act to generate or augment the signs of adaptive trans-generational effects (Fig. 3b).

Here, we have focused on trans-generational effects. Yet, we would also like to stress that the problem outlined here applies equally well to within-generational anticipatory effects. For instance, experiencing a specific environment early in life may trigger developmental pathways that make the adult phenotype particularly apt in similar environmental conditions. As they are conceptually similar (cf., e.g. Monaghan 2008), it is easy to realize that a match/mismatch experiment testing environmental matching within generations will share the same weaknesses as the trans-generational approach.

A remedy suggestion – an experimental control

Above we mentioned in passing that the drawback of the reciprocal match/mismatch approach is that principally, it needs an additional experimental control. At first sight, this argument may seem unreasonable – How can it be that this fully factorial design lacks an experimental control? The problem lies in the potential ‘silver-spoon’ (or ‘carry-over’) effect. ‘Silver-spoon’ effects are non-anticipatory; hence, they are non-contextually transmitted. Yet, we have seen that their *influence* may be context-dependent, hence non-additive and instead environment-dependent (Semlitsch & Gibbons 1990; Fox 2000; Svensson & Sinervo 2000; Oksanen *et al.* 2003; Dziminski & Roberts 2006; Krist & Muncinger 2015). Thus, the match/mismatch design does not control for context-dependent ‘silver-spoon’ effects. Therefore, we need to experimentally control for ‘silver-spoon’ effects as we have seen that a statistical control will be inefficient. Potentially, there are more solutions, yet we have identified two principle approaches in which this may be achieved – depending on the circumstances, these approaches will be more or less demanding.

As the problem is associated with uncontrolled ‘silver-spoon’ effects, we need to find means to control for them. One way would be to treat the parent generation identically (e.g. nutritionally), yet experimentally manipulate their perception of the expected future environment relevant for offspring development. This may prove challenging as one would have to influence environmental perception without changing the environment *per se*. Nevertheless, in cases where environmental cues are unrelated to any stimuli affecting potential ‘silver-spoon’ effects, this could indeed be practicable. To illustrate this, let us consider two examples. Daylength is often a reliable cue used to perceive seasonal environmental change (Mousseau & Dingle 1991). Thus, by exposing the parental generation to varying daylengths and subsequently rear offspring in environments matching or non-matching, this parental

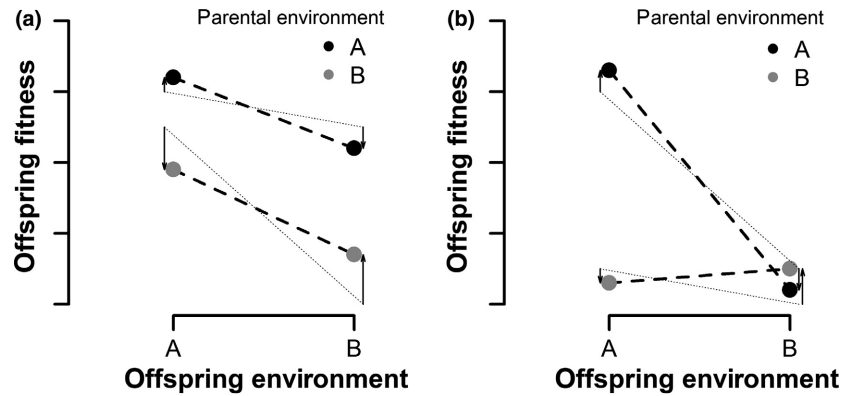


Fig. 3. Illustration showing the expected measurable outcome (dots and dashed lines) from a match/mismatch experiment performed under (a) beneficially saturated and (b) detrimentally saturated conditions, respectively. As in Fig. 1, the dotted lines indicate expectations without anticipatory parental effects, whereas the arrows indicate changes due to the match or mismatch of parent–offspring environments. Note that under beneficially saturated conditions, the experiment may show no apparent signature of adaptive parental programming (see parallel dashed lines), even though the effect is clearly there (see arrows). Under detrimentally saturated conditions, the experiment would reveal very clear signs of anticipatory parental effects. Yet, the pattern is caused primarily by environment-dependent ‘silver-spoon’ effects.

information would provide data able to examine the possibility of adaptive parental programming. In our view, this is uncontroversial as long as experiencing different daylengths does not affect parents’ ability to provide offspring with ‘silver-spoon’ benefits that may have different effects depending on offspring environment. For daylength, this seems a valid assumption. However, temperature may equally well provide parents with information about future environmental conditions (see, e.g. Mousseau & Dingle 1991). Yet, varying temperature may not prove such a good idea, as temperature is likely to affect metabolic rate, energy expenditure and thus parental size and/or condition as well (see, e.g. Atkinson & Sibly 1997). In this example, temperature, but not daylength, would be an environmental cue potentially affecting parental provisioning and hence represent an uncontrollable ‘silver-spoon effect’. This would potentially bias the results impeding any firm conclusions.

Another way to avoid uncontrollable ‘silver-spoon effects’ would be to directly manipulate parental cues instead of doing it indirectly via parental perception. To do this, one would obviously need to know the proximate mechanism by which phenotypic plasticity may be trans-generationally mediated (e.g. via maternal hormones, see Groothuis *et al.* 2005; Ruuskanen 2015). This has the huge benefit that one avoids *confounding* parental effects altogether, enabling a distinct demonstration of adaptive trans-generational phenotypic plasticity. This argument also highlights the potential pitfall of treating phenotypes as ‘black boxes’ ignoring the proximate mechanisms shaping them. In our view, manipulation of the parental signal provides a much more direct test of trans-generationally mediated phenotypic plasticity than the outcome of a match/mismatch experiment. The importance of manipulating the developmental input rather than the environment for testing adaptive developmental plasticity has recently also been highlighted by Nettle & Bateson (2015). However, a word of caution is needed on this point: This alternative requires that the signalling mechanism underlying the parental effect is genuinely well understood.

Failure to manipulate and reproduce parental mimicking control of the signal may introduce severe experimental artefacts, where the effects are difficult to evaluate. In particular, when the developmental input consists of a signalling complex, manipulation of single signal components may lead to ontogenetic incompatibilities with other elements of the signalling complex. Nevertheless, manipulating parental signals rather than parental environment has an additional advantage. As we outlined above, the match/mismatch approach provides one single estimate of the anticipatory parental effects – the interaction term. Thus, anticipatory parental effects are inherently assumed to be equal in magnitude across environments – note that all arrows in Fig. 1c, indicating adaptive trans-generational plasticity, are of equal size, depicting the deviation from the additive effects of parental and offspring environment. This is a strongly restrictive assumption, as fitness effects due to parental programming may be environment-dependent – receiving the wrong signal may be disastrous in some environments but just slightly detrimental in others. Manipulating parental cues indeed makes it possible to infer differences in the magnitude of adaptive trans-generational effects in different environments (note the differently sized arrows in Fig. 3).

Although manipulating parental cues in our view provides the *ideal* theoretical solution, we realize that it may not always be practicable, or even introduce more serious problems if the model system is not well understood. In such cases, we would recommend researchers to estimate environment-dependent ‘silver-spoon’ effects in independent control experiments. Given that the source of the silver-spoon effect (e.g. egg size, parental care) is known, one could look for naturally occurring variation in these traits and thereby assess its effect in each separate offspring environment. We do not consider this the ideal solution. However, in situations, where no other solution seems applicable, this can provide an easily accessible possibility to assess the magnitude of the ‘silver-spoon’ effect and compare this to the results from the match/mismatch experiment.

Concluding remarks

Possibly, the lack of an effect was due to the fact that the study was performed under benign laboratory conditions (or, in case of field studies, during a particularly “good year”)

These, or similarly worded, arguments are common in discussions and criticisms of evolutionary and behavioural ecology studies failing to find any negative effects of stressors despite strong *a priori* expectations. The argument is applicable for numerous moderators, such as the lack of ‘good-genes’ benefits of mate choice (e.g. Schmolli *et al.* 2005), the absence of detrimental inbreeding effects (e.g. Richardson, Komdeur & Burke 2004; Fox & Reed 2011), no cost of parasitic infection (e.g. Bedhomme *et al.* 2004), no effect of parental care or other parental effects (e.g. Wedell & Arak 1989), weak effect of large propagule size (e.g. Fox & Mousseau 1996). In principle, the above argument is based on the assessment that environmental effects can be beneficially saturated. Our line of reasoning here is thus not new, and it has quite clearly been acknowledged that independent environmental effects do not necessarily have to act additively on survival and reproductive success. Here, we have shown, however, that additivity of environmental effects is a crucial underlying assumption of match/mismatch experiments testing whether organisms are capable of adaptive trans-generational phenotypic plastic responses. This may lead to both apparent underestimates (see Fig. 3a) and overestimates (see Fig. 3b) of parental programming depending on the nature of the underlying environmental interaction. One could possibly make a case that beneficially saturation is a more common phenomenon than detrimentally saturated environmental effects. In that case, anticipatory parental effects will be downward biased. This would apply to both individual and meta-analytical studies. Thus, the notion that the current experimental evidence does not support a widespread occurrence of anticipatory parental effects in nature (Uller, Nakagawa & English 2013) may eventually be somewhat misleading (see also Burgess & Marshall 2014).

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Data accessibility

This manuscript does not include any data.

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