Received: 17 July 2017 | Accepted: 19 September 2017

DOI: 10.1111/2041-210X.12906

FORUM

Methods in Ecology and Evolution — BRITISH ECOLOGICAL SOCIETY

Adaptive parental effects and how to estimate them: A comment to Bonduriansky and Crean

Leif Engqvist[1] | **Klaus Reinhold**[2]

[1]Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

[2]Evolutionary Biology, Bielefeld University, Bielefeld, Germany

Correspondence
Leif Engqvist
Email: leif.engqvist@iee.unibe.ch

Handling Editor: Matthew Davey

Abstract

1. To fully understand the evolution of adaptive parental effects we need to reliably estimate their magnitude.
2. Recently, we (Engqvist & Reinhold, 2016, *Methods in Ecology and Evolution*, **7**, 1482) highlighted some important problems when estimating the magnitude of anticipatory parental effects in the so-called match/mismatch experiments. As the signature of such parental effects is a statistical interaction between parental environment and offspring environment, it will be difficult to disentangle these effects from other effects depending on a combination of parental and offspring environment, such as context-dependent silver-spoon (= condition-transfer) effects.
3. In a recent article, Bonduriansky and Crean (2017, *Methods in Ecology and Evolution*) suggested to manipulate environmental quality on a continuous scale and using a geometric framework as a way out of this dilemma.
4. Here, we highlight and discuss the benefits and potential drawbacks of the suggested method. We conclude that using this approach, one may extract more detailed information but unfortunately, it will not resolve the interpretive ambiguity inherent in this experimental design.

KEYWORDS
adaptive parental effects, condition-transfer, silver-spoon effects, statistical interactions

In their article, Bonduriansky and Crean (2017) make some very important and insightful remarks on the study of parental effects. We certainly agree with the tenor of the article arguing that the study of parental effects will gain by focussing more on the potential adaptive value of what they refer to as condition-transfer effects and welcome this scientific discussion. Nevertheless, as we identified a few potentially confusing issues regarding the final part of the article, where they introduce the geometric framework as a means to study adaptive parental effects, we feel that this comment is necessary.

Very recently, we highlighted an important pitfall regarding the experimental design aimed to study anticipatory parental effects (Engqvist & Reinhold, 2016). Such parental effects are similar to condition-transfer effects—also referred to as carry-over effects or silver-spoon effects (Uller, Nakagawa, & English, 2013)—in that they both constitute trans-generationally induced phenotypic plasticity in offspring. However, these two parental effects are also inherently different. Condition-transfer indicates that parent condition will induce higher offspring condition irrespective of offspring environmental quality (yet importantly, the magnitude may be context-dependent). Anticipatory effects, on the other hand, crucially depend on a match between parent and offspring environmental quality. The concern we expressed in our article (Engqvist & Reinhold, 2016), is that in a two-factorial design varying parental and offspring environmental quality, the two parental effects will be statistically confounded. For a full treatment of this, we refer the reader to our original article. Shortly stated, the problem is that this experiment cannot disentangle between anticipatory parental effects and context-dependent condition-transfer-effects. For example, it may signify anticipatory effects if offspring are doing relatively better in a good quality environment if their parents came from a similar environment, but it may equally well indicate that condition-transfer effects are more pronounced in good quality environments.

To solve this problem Bonduriansky and Crean (2017) suggest to expand the level of measurements so that both parental offspring environmental factors span a broad range of levels. By analysing the data within a geometric framework, they argue that it will be possible to detect complex interactions and nonlinear effects. They further assure the reader that "[…] 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." They summarize their argument by stating "[…] 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." This is a very strong argument, and as such, this would indeed be a tremendous progress to the current state-of-the-art. Unfortunately, Bonduriansky and Crean (2017) provide very little details to support their argument and we therefore decided to examine it in detail.

In abstract theoretical terms, we can express parental carry-over effects combined with immediate offspring environmental effects. Assuming clonal reproduction and negligible genetic variation, the expected offspring phenotype (Y) can be written as follows: $Y = f_P(x_p) + f_O(x_O) + f_{P \times O}(x_P, x_O)$ (cf. e.g. Kuijper & Hoyle, 2015). Here, x_p and x_O describes the parental and offspring environmental quality, respectively; the f_P and f_O are functions that describe the phenotypic effect of these, that is, the parental condition-transfer and immediate offspring environmental effects. Finally, $f_{P \times O}$ is a function that describes in which way the magnitude of potential condition-transfer effects depends on the offspring environment. If we add the influence of anticipatory parental effects, we end up with a very similar expression: $Y = f_P(x_P) + f_O(x_O) + f_{P \times O}(x_P, x_O) + f_{AE}(x_P, x_O)$. Here f_{AE}

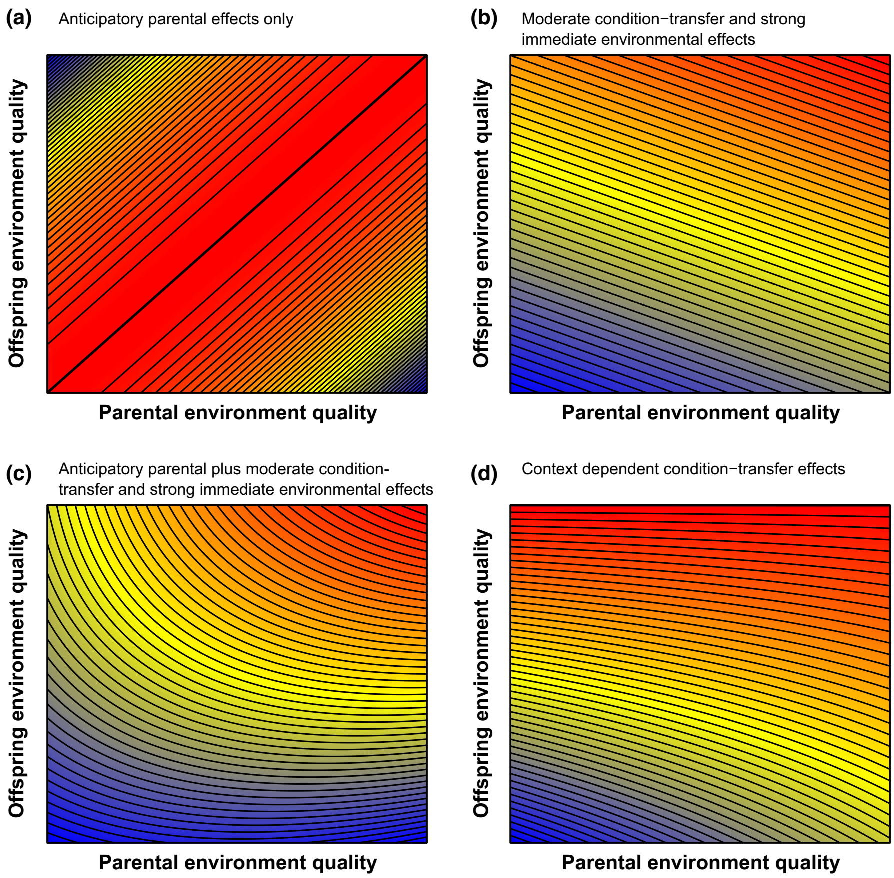

FIGURE 1 Schematic illustrations of four different outcomes, using a geometric framework. Colours depict increasing offspring fitness from low (blue) to high (red). Lines are iso-fitness lines. In (a) a spotless anticipatory parental effect scenario is illustrated. Offspring are always doing best the more similar the environment is to the one experienced by their parents. In (b) a situation is depicted where moderate condition-transfer effects (seen as a subtle rise on the horizontal plane) and strong immediate offspring environmental effects (seen as an obvious rise on the vertical plane) act additively. In (c) the effects from (a) and (b) are combined. The anticipatory effects are less obvious but the interaction is still visible as concave iso-fitness lines causing a ridge in the *xy*-plane. In (d) there are no anticipatory parental effects and the condition-transfer effects are context-dependent, being stronger if offspring environmental quality is poor than when offspring environmental quality is good. This interaction is visible as convex iso-fitness lines causing a depression in the *xy*-plane. Clearly, such context-dependent condition-transfer effects will statistically obscure true anticipatory parental effects. Parameter values: (a) $f_P = f_O = f_{P \times O} = 0$, $f_{AE} = 2 \cdot x_P x_O - x_P^2 - x_O^2$; (b) $f_P = x_P$, $f_O = 2.5x_O$, $f_{P \times O} = f_{AE} = 0$; (c) $f_P = x_P$, $f_O = 2.5x_O$, $f_{P \times O} = 0$, $f_{AE} = 2 \cdot x_P x_O - x_P^2 - x_O^2$; (d) $f_P = x_P$, $f_O = 2.5x_O + f_{P \times O} = -x_P x_O$, $f_{AE} = 0$; see text for further details

describes the phenotypic effect attributable to the match/mismatch of parent-offspring environments, that is, the anticipatory parental effects.

What is important is that the effect of $f_{P \times O}$ and f_{AE} will be statistically confounded within the parent-offspring-environment-interaction. They are both bivariate functions of the parental and the offspring environmental quality and it is therefore not possible to vary them independently from each other in a straightforward manner. As can be seen from the equation above, this does not depend on the scale of measurement of either parental environment (x_p) nor offspring environment (x_O). It thus does not matter for our argument whether environmental quality is measured on a discrete scale (such as good/bad) or on a continuous scale. In Engqvist and Reinhold (2016), we illustrated the problem using the discrete case. The problem remains for the continuous case (see Figure 1), contrasting Bonduriansky and Crean's (2017) argument that this would solve the problem.

In summary, we do not want to discourage researchers interested in adaptive parental effects to use the geometric framework as outlined by Bonduriansky and Crean (2017). Certainly, a more fine-tuned experimental variation in parental environmental quality will allow for a more fine-tuned investigation of its effects, such as the detection of nonlinear patterns, not feasible with a simple two-factorial design. Nevertheless, it will not by itself resolve the problematic issue previously outlined by us (Engqvist & Reinhold, 2016). It may be possible to reveal complex interactions using the geometric framework. However, it cannot reveal causality, that is, whether anticipatory effects or context-dependent condition-transfer effects are causing the statistical interaction. We argue that sophisticated experimental controls are necessary for this purpose, as outlined in detail in Engqvist and Reinhold (2016).

AUTHORS' CONTRIBUTIONS

L.E. and K.R. together discussed the arguments and the general outline. L.E. drafted the first version of the manuscript and K.R. provided comments and finalised it.

DATA ACCESSIBILITY

This manuscript does not include any data.

ORCID

Leif Engqvist http://orcid.org/0000-0002-9434-7130

REFERENCES

Bonduriansky, R., & Crean, A. J. (2017). What are parental condition-transfer effects and how can they be detected? *Methods in Ecology and Evolution*, https://doi.org/10.1111/2041-210X.12848.

Engqvist, L., & Reinhold, K. (2016). Adaptive trans-generational phenotypic plasticity and the lack of an experimental control in reciprocal match/mismatch experiments. *Methods in Ecology and Evolution*, *7*, 1482–1488.

Kuijper, B., & Hoyle, R. A. (2015). When to rely on maternal effects and when on phenotypic plasticity? *Evolution*, *69*, 950–968.

Uller, T., Nakagawa, S., & English, S. (2013). Weak evidence for anticipatory parental effects in plants and animals. *Journal of Evolutionary Biology*, *26*, 2161–2170.

How to cite this article: Engqvist L, Reinhold K. Adaptive parental effects and how to estimate them: A comment to Bonduriansky and Crean. *Methods Ecol Evol*. 2017;00:1–3. https://doi.org/10.1111/2041-210x.12906