



# Adaptive parental effects: the importance of estimating environmental predictability and offspring fitness appropriately

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Anticipatory parental effects (APE's) occur when parents adjust the phenotype of their offspring to match the local environment, so as to increase the fitness of both parents and offspring. APE's, as in the evolution of adaptive phenotypic plasticity more generally, are predicated on the idea that the parental environment is a reliable predictor of the offspring environment. Most studies on APE's fail to explicitly consider environmental predictability so risk searching for APE's under circumstances where they are unlikely to occur. This failure is perhaps one of the major reasons for mixed evidence for APE's in a recent meta-analysis. Here, we highlight some often-overlooked assumptions in studies of APE's and provide a framework for identifying and testing APE's. Our review highlights the importance of measuring environmental predictability, outlines the minimal requirements for experimental designs, explains the important differences between relative and absolute measures of offspring fitness, and highlights some potential issues in assigning components of offspring fitness to parental fitness. Our recommendations should result in more targeted and effective tests of APE's.

Synthesis

A decent set of theory is available to understand when certain kinds of parental effects might act to increase parental fitness (i.e. be 'adaptive'). This theory could be better incorporated into empirical studies on anticipatory parental effects (APE's). Here, we provide practical advice for how empirical studies can more closely align with the theoretical underpinnings of adaptive parental effects. In short, robust inferences on APE's require quantitative estimates of environmental predictability in the field over the space and time scales relevant to the life history of the study organism as well as an understanding of when to use absolute or relative offspring fitness.

Parental effects occur when the environment or phenotype of the mother or father influences the phenotype of their offspring (Badyaev and Uller 2009, Bonduriansky and Day 2009, Wolf and Wade 2009). Parental effects are just another form of phenotypic plasticity ('transgenerational plasticity') where the phenotypic change in offspring occurs in response to the parental environment or phenotype, rather than the offspring environment (Mousseau and Fox 1998). Like plasticity, parental effects are not always adaptive. While parental effects can affect both parental and offspring fitness simultaneously, they are typically considered adaptive when they enhance parental fitness (Marshall and Uller 2007). One type of adaptive parental effects is anticipatory parental effects (APE's), whereby parents modify the phenotype of their offspring in response to changes in the environment that act to increase parental fitness by also increasing offspring fitness. APE's are expected to occur in situations when the environmental conditions that offspring encounter are sufficiently predictable from the parental environment or phenotype.

Importantly, APE's are not the only form of adaptive parental effects that might be observed in response to changes in the parental environment. Consistent with general life history theory (Stearns 1992), parents may respond to environmental change by reducing offspring fitness in order to increase the long term fitness returns that parents achieve ('selfish parental effects' sensu Marshall and Uller 2007). Furthermore, when parents, especially those that only reproduce once, cannot predict their offspring's environment, they may instead produce a range of offspring phenotypes in order to decrease the variance in fitness returns ('bet-hedging parental effects' sensu Marshall and Uller 2007, see also Einum and Fleming 2004, Marshall et al. 2008, Fischer et al. 2010). While both selfish and bet-hedging parental effects can be adaptive, we will not consider these here further, but note them to highlight that parental effects do not always act to increase offspring fitness (Marshall and Uller 2007).

Interest in APE's has grown rapidly in recent years and for good reasons. From an evolutionary perspective,

nongenetic inheritance is increasingly recognized as an important modifier of evolutionary trajectories (Kirkpatrick and Lande 1989, Uller 2008, Bonduriansky and Day 2009). From an ecological perspective, APE's can have important consequences for population dynamics (Benton et al. 2001, 2005, Plaistow et al. 2006) and may increase the likelihood of population persistence in the face of environmental change (Chevin and Lande 2010, Ezard et al. in press). In particular, a number of studies have demonstrated that APE's may buffer offspring from the negative consequences of environmental stressors associated with climate change (Parker et al. 2009, Miller et al. 2012, Salinas and Munch 2012, Munday et al. 2013). Accordingly, the number of studies exploring APE's is increasing rapidly and APE's have now been demonstrated in a range of systems and taxa (Uller et al. 2013). In particular, foundational studies in this field provide compelling evidence for just how much control parents (mothers in particular) can exert on the phenotype of their offspring. For example, seed beetle mothers reared on seeds with a thick seed coat produce offspring that are larger and better able to burrow into the seed than offspring from mothers reared on seeds with a thin seed coat (Fox et al. 1997). *Daphnia* reared in the presence of a predator produce predation-resistant offspring (Agrawal et al. 1999). Understorey forest herbs grown in the shade produce shade-resistant offspring (Galloway and Etterson 2007). Marine bryozoans experiencing high competition produce more competitive and more dispersive offspring (Allen et al. 2008). In each of these studies, it appears that mothers can shift the phenotype of their offspring such that the negative effects of a more stressful or difficult environment are minimized.

While there are spectacular examples of APE's, a recent meta-analysis revealed weak evidence for APE's in the literature overall (Uller et al. 2013). Uller et al. (2013) identified several reasons why the evidence for APE's might be limited and, in particular, suggested that there may be some methodological reasons for the lack of evidence for APE's in many systems; a suggestion with which we strongly agree. Here, we wish to highlight some often-overlooked assumptions in studies of APE's and provide a framework for identifying and testing APE's. We will assume that readers are familiar with the original paper proposing APE's (Marshall and Uller 2007) as well as the recent meta-analysis by Uller et al. (2013). Note that we extend the term 'anticipatory maternal effects', or AME's, originally used in Marshall and Uller (2007) to acknowledge the importance of paternal effects in addition to maternal effects (Uller 2008, Crean et al. 2013). Our review highlights the importance of measuring environmental predictability: a key but largely overlooked aspect in studies inferring APE's. We also outline the minimal requirements for experimental designs, explain the important differences between relative and absolute measures of offspring fitness, and highlight some important but unresolved issues in assigning components of offspring fitness to parental fitness.

### Minimum experimental design needed to infer APE's

As outlined in Uller et al. (2013), orthogonal manipulations of the offspring and parental environments are necessary to

draw inference on the adaptive significance of parental effects. Ideally, genetic lineages (or 'families') should be reared in a quantitative genetic design for multiple generations prior to beginning the experiment to equalize parental environmental effects between families (Agrawal 2002). In many instances however, rearing over multiple generations is challenging, so as a more pragmatic alternative, individuals can be randomly sampled from a field population and then randomly allocated to one of at least two environments (e.g. warm and cool temperatures; Burgess and Marshall 2011). For this alternative approach to be useful however, a number of conditions must be met. First, mortality of parents should be absent in all parental environments, so that any changes in offspring phenotype can be attributed to plasticity, rather than the potentially confounding effects of selection. Second, also to avoid selection effects, all parents in the experimental population need to provide offspring. If some parents in the experiment do not produce offspring, there is a risk that comparisons of offspring fitness will be biased if the parents not reproducing are a nonrandomly selected genotype. Situations where individuals may survive but not produce offspring might be especially likely when the parental environments vary in levels of stress. More complicated designs may be necessary to ensure that there are no selection effects and to unequivocally ascribe any effects as parental effects (e.g. by splitting and switching experimental individuals between orthogonal treatments, see Jensen et al. in press for an example).

After a period of time relevant to the duration at which parents can respond to the environment and influence offspring phenotype, the clutch of offspring from each parent needs to be split between at least two environments (Fig. 1 in Uller et al. 2013). The type (e.g. environment A vs environment B) or state (high value of environment A vs low value of environment A) of the environment need not be the same between the parental and offspring treatments. Consideration, however, needs to be given to the likely environments that parents and offspring encounter in the field and the environment providing the cue in the parental environment (e.g. the chemical scent of a predator) and the agent of selection in the offspring environment (e.g. the predator itself; if the chemical cues themselves have no effect on fitness, but see Trussell et al. 2003). Often developmental cues and selective environments are correlated (Alekseev and Lampert 2001), so the chosen parental and offspring environmental type or state will often be the same.

A measurement of some component of offspring fitness (e.g. survival) is required to infer whether the parental effect is adaptive. Survival may often be the most relevant component of offspring fitness to measure, but the measured component of fitness should of course be the one most relevant to the biology of the study species because different components of fitness may give different inferences on APE's (van Tienderen 1991). Importantly though, simply measuring the phenotypes of offspring provides no information on APE's unless those phenotypes have demonstrated links to fitness in the environment in which offspring encounter. For example, larger offspring do not always have the greatest performance in every environment that they are likely to encounter (Kaplan 1992). As such, inferring that an increase in offspring size (a change in off-

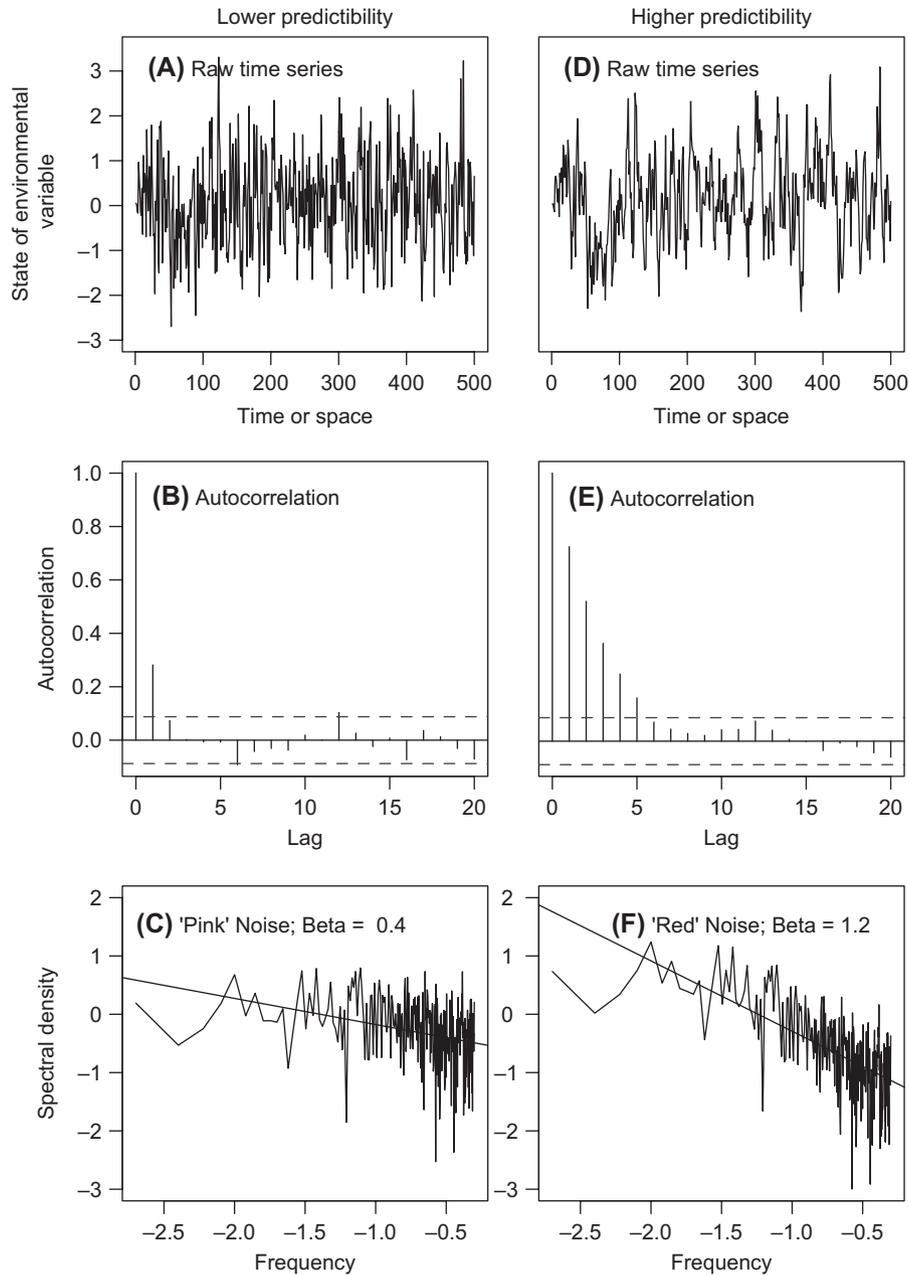


Figure 1. Two simulated data series (e.g. temperature variation in time) with the same variability, but low (left column; A–C) or high (right column; D–F) predictability. Interpretation of such data depends on the biology of the study species and how individuals perceive the environmental variable in the data series. Both situations (i.e. left and right columns) may represent a predictable environment to a species in which the duration of offspring development (or spatial scale of offspring dispersal) is 1 time (or space) unit. On the other hand, only the higher predictability scenario (right column) will be predictable for a species in which the duration of offspring development (or spatial scale of offspring dispersal) is between 1 and 5 time (or space) units. Data series were simulated using an auto-regressive (AR) process:  $\rho x_t + \omega_t \sqrt{1 - \rho^2}$ , where  $\rho$  is the autocorrelation,  $x_t$  is the environmental state at time  $t$ , and  $\omega_t$  is a random standard normal variable.

spring fitness) in response to changes in the maternal environment should not be assumed to be adaptive in the absence of estimates of the offspring size–fitness relationship in that specific environment

### Environmental variability and predictability

Central to any discussion about adaptive plasticity (be it transgenerational or otherwise) is the requirement that

the environment is both variable and predictable (DeWitt et al. 1998, Donohue and Schmitt 1998, Scheiner and Holt 2012). Because a variable environment can range from completely predictable to completely unpredictable (Ruokolainen et al. 2009) (Fig. 1), measuring environmental variability (e.g. using the coefficient of variation) does not provide a measure of predictability. Importantly, variability and predictability should also be considered relative to the spatial and temporal scales relevant to the biology of the

study organism. Environments that are predictable to a species with a relatively short duration of gamete/offspring development and parental care (or relatively short dispersal distances) may be unpredictable to a species with a relatively longer duration (or relatively greater dispersal distance, Fig. 1). Populations occurring in environments that are constant at the scale at which individuals experience them are unlikely to evolve (transgenerational) plasticity (DeWitt et al. 1998, Scheiner and Holt 2012). Similarly, populations that experience completely unpredictable and variable environments are unlikely to evolve APE's because parents can only match the phenotype of their offspring to the offspring's local environment if they can anticipate the environment their offspring will experience (Fischer et al. 2010, Donald-Matasci et al. 2013).

Predictability is a key but largely overlooked point in studies on APE's – APE's will only be favored if the parental environment is a good predictor of the offspring environment in space or time (Donohue and Schmitt 1998, Galloway 2005). Most studies manipulate parental environments without explicit reference to whether that manipulation represents a reliable signal to parents that is likely to predict the environmental state that offspring experience. Uller et al. (2013) found that, of the 58 studies on APE's they reviewed, only seven provided data or cited papers with data that demonstrated environmental predictability between parent and offspring environments. In a rare example, Galloway (2005) showed that the scale of seed dispersal in an understory forest herb was less than the typical distance between light gaps, suggesting that the maternal light environment was a good predictor of the offspring light environment and that anticipatory maternal effects occurred in this species (Galloway and Etterson 2007). While Galloway (2005) addressed the issue of predictability explicitly, and made a sound and convincing case that parental environments are likely to be good predictors of offspring environments in their study species, even this excellent study did not formally quantify environmental predictability (see Burgess and Marshall 2011 for a study that did formally quantify environmental predictability). Studies of APE's risk manipulating parental environments that may vary, but are poor predictors of offspring environments, essentially searching for APE's under circumstances where APE's are unlikely to occur. We believe this failure to quantify environmental predictability is widespread in the literature and is one of the major reasons for mixed evidence generated by some APE studies (Uller et al. 2013). Obviously, measuring predictability is not necessary in instances where the offspring environment is perfectly predictable from the parental environment and parents have enough time to respond to cues. Such instances seem likely in the case of oviposition site selection where, in the case of the generalist parasitic seed beetle *Stator limbatus* for example, mothers lay their eggs directly onto the host seed and, upon hatching, the larvae burrow into the seed where they complete development and emerge as adults (Fox et al. 1997). We suspect, however, that such conditions are relatively rare in most other taxa and suggest that, at the very least, a case for environmental predictability should be presented.

## Quantifying environmental predictability

How can the predictability of the offspring environment be formally quantified? Fortunately, there are specific tools for quantifying the degree to which current conditions predict the state of future conditions (Colwell 1974, Stearns 1981, Legendre and Legendre 1998, Pinheiro and Bates 2000, Ruokolainen et al. 2009). In essence, the tools allow a researcher to quantify the temporal or spatial scale at which conditions are similar; where conditions are expected to be different beyond that scale. At the broadest level, the tools to use depend on whether environments vary in time or in space and are continuous (quantitative, e.g. temperature) or discrete (qualitative, e.g. presence or absence of a predatory or herbivore). Environmental variation in both space and time is likely to be relevant when, for example, offspring disperse or adults move between locations to release offspring. For the sake of clarity, we will discuss temporal and spatial predictability separately. Our aim is not to provide a prescriptive recipe, but to increase awareness of some possible quantitative approaches.

### Predictability in time

For quantifying environmental predictability of quantitative variables in time, correlograms, spectral analysis, or wavelet analysis can be used (Legendre and Legendre 1998). Correlograms are plots of the autocorrelation between successive terms in a data series, which measures the dependence of values in the series on the values before it (at a distance of  $k$  lags). For example, we calculated correlograms from time series data of water temperature in the field to show that temperature on any given day was a good predictor of the temperature up to 15 days into the future (Burgess and Marshall 2011). Given that individuals of our study species, a marine bryozoan, brood offspring for approximately seven days, the temperature that mothers experience while brooding is a good predictor of the temperature their offspring will experience during dispersal and early post-settlement growth.

Spectral analysis builds on correlograms to provide more information. Spectral analysis identifies the dominant frequencies comprising a time series by determining how much of the variance in the time series is associated with different frequencies. Environmental predictability can be estimated using discrete time auto-regressive (AR) processes (in the time domain) (Ripa and Lundberg 1996), sinusoidal processes (in the frequency domain) (Halley 1996), or moving averages (Legendre and Legendre 1998, Pinheiro and Bates 2000). Each method assumes a different correlation structure between events, so thought must be given to inferences on predictability relevant to APE's using the different methods (Legendre and Legendre 1998, Pinheiro and Bates 2000). Correlation structures may have important implications for interpreting APE's, as they have for population dynamics (Cuddington and Yodzis 1999).

Sinusoidal processes assume that variance scales with frequency ( $f$ ) according to an inverse power law,  $1/f^\beta$  (Vasseur and Yodzis 2004, Ruokolainen et al. 2009). Unpredictable, or random, variation (also called white noise) occurs when  $\beta = 0$  indicating that there is an equal mix of cyclic components at all frequencies in the variance

spectra. Increasing environmental predictability, or autocorrelation, in the time series (also called colored noise) is given by increasing values of  $\beta$  indicating that the time series is dominated by frequencies in a certain range. Specifically,  $0.5 < \beta < 1.5$  (red noise) is dominated by low frequency (or long-period) cycles and has residuals that are autocorrelated. Such noise indicates more predictable environments and an increased probability of having long runs of above or below average conditions (compared to white noise environments).

Wavelet analysis is an extension of spectral analysis; it is effectively a localized spectral analysis in that instead of estimating the variance spectrum of the entire (stationary) time series, it estimates the frequency spectrum at each point in the time series. Wavelet analysis reveals changes in the frequency spectra through time and is particularly useful for examining the consequences of changes in cues over time (e.g. timing of spring transition changing across years) (Legendre and Legendre 1998, Torrence and Compo 1998).

#### **Data requirements**

The minimum number of observations and the time interval between observations in the time series of environmental data should be guided by the biology of study species and the characteristics of the environment of interest (e.g. in the case of *Bugula neritina*, it was the period when *B. neritina* are particularly common in the field site as well as the duration of brooding; Burgess and Marshall 2011). For any time series, the observational window over which inferences can be made about environmental predictability is  $2\Delta$  to  $(n\Delta)/2$ , where  $\Delta$  is the interval between consecutive observations and  $n$  is the number of observations in the time series. All observations need to be regularly spaced in time. Smoothing functions can be fit to data collected at irregularly time intervals and interpolation methods used to create a new data series with evenly spaced observations (Legendre and Legendre 1998).

#### **Predictability in space**

For quantifying environmental predictability of quantitative variables in space, spatial autocorrelation statistics like Moran's  $I$  or Geary's  $c$  can be used (Legendre and Legendre 1998). Such statistics require observations of the environmental variable at a range of sites as well as a matrix containing the geographical distances between each pair of sites. A spatial correlogram, similar to a temporal correlogram discussed above, can then be constructed by plotting the spatial autocorrelation coefficients (vertical axis) for each distance class (irregularly spaced observations are grouped into distance classes on the horizontal axis). The distance at which the autocorrelation coefficients are no longer significant indicates the spatial scale of environmental predictability. Similarly, a sample variogram can be constructed by plotting the semi-variance, which is the variance of the difference between observed values at two locations, (vertical axis) for each distance class (horizontal axis). The spatial scale of autocorrelation can be identified by the distance class at which the semi-variance levels off; at which point environments beyond that spatial scale are no longer correlated.

To be useful for understanding APE's however, spatial autocorrelation structures need to be assessed in relation

to the way that organisms experience the spatial environment through offspring dispersal (Levins 1968, Lechowicz and Bell 1991, Galloway 2005). Finally, with the same data used to estimate the predictability of the spatial environment, it is important to also estimate the frequency of different environments because, depending on the 'softness' of selection, the frequency of environments will also influence the interpretation of APE's (Lechowicz and Bell 1991, Gomulkiewicz and Kirkpatrick 1992, Kelley et al. 2005). Ideally, this frequency distribution would be weighted by an estimate of the offspring dispersal kernel of the parent to better indicate how the parent 'accesses' these different environmental states. More advanced discussion of methods to quantify spatial and temporal predictability, and different correlation structures, can be found in Legendre and Legendre (1998) and Pinheiro and Bates (2000).

#### **Predictability of discrete environments**

The methods proposed above may be applied to any environmental state known or suspected to be periodic or cyclic in time or space. However, some environmental cues relevant to APE's are likely to be discrete, or qualitative (e.g. presence or absence of a predatory or herbivore). Various types of spatial autocorrelation coefficients exist for quantifying environmental predictability of qualitative variables in space, but their description is beyond the scope of this short paper (we refer the reader to Colwell 1974, Sakai and Oden 1983, Legendre and Legendre 1998, Dwyer et al. 2010). Predictability of qualitative variables in time can be estimated by calculating the probability of an event occurring, using approaches relying on probability distributions or Markov chain processes. We think however, that very few environments relevant to APE's are truly discrete, even though such environments are often treated as discrete in experimental designs. For example, the presence/absence of a predator may be discrete, but in nature, most organisms will experience predation risk on a continuum because predator abundance also varies.

#### **Correlations between the environmental cue and the agent of selection**

In some instances, the environmental cue that mothers detect and respond to may be a different environment to the agent of selection on offspring phenotypes. For example, photoperiod may represent a cue to *Daphnia* parents about the subsequent food abundance for their offspring (Alekseev and Lampert 2001). Several approaches exist to quantify temporal autocorrelation of two or more time series as well as ways to distinguish causality from correlation between environments and cues (Sugihara et al. 2012). For two time series, the gain spectrum can be estimated to assess the relationship between two time series, which is analogous to a coefficient of a simple linear regression. For multiple time series, the method is called principal components in the frequency domain, where the spectrum is estimated for each linear combination of the multiple time series (see Legendre and Legendre 1998 p. 683 for further reading).

We recognize that our suggestion to formally analyze predictability increases the burden of data collection and analysis substantially. We further acknowledge that one of us (DJM) in particular has failed to analyze predictability in most of his previous studies of APE's. Despite these

issues, we now make the recommendation to think more formally about environment predictability because as both empiricists and reviewers, we have seen too many studies where the potential for APE's was exceedingly poor such that, in many instances, the effort to search for such effects was essentially doomed before it began. Furthermore, given advances in remote sensing and data logging, the spatial and temporal variation in many physical variables can be collected relatively cheaply and easily such that empiricists have much greater access to such data relative to just a few years ago.

### **Measuring offspring fitness appropriately**

In addition to measuring environmental predictability, measuring offspring fitness appropriately is also an important and overlooked aspect in studies on APE's. Measuring selection and offspring fitness appropriately is important because it sheds light on the relative importance of the frequency of different environments, in addition to the predictability of the environment. In particular, when offspring disperse, the relative importance of hard and soft selection (defined below) will determine whether it is appropriate to compare components of offspring fitness within (relative) or among (absolute) offspring environments. Furthermore, incorrectly assigning offspring fitness to parents can give incorrect estimates of selection on parental traits.

#### ***Relative versus absolute offspring fitness in spatially varying environments***

Inferences about the adaptive significance of parental effects in spatially heterogeneous environments, especially when offspring disperse at early developmental stages, depend on the characteristics of the life cycle (Burgess and Marshall 2011). If offspring disperse to a range of different environments, and there is environment-specific selection on offspring phenotypes followed by density-dependent mortality within each environment, selection is said to be frequency-dependent ('soft' selection; Levene 1953, Wallace 1975). Because density-dependent mortality occurs after selection, the contribution of offspring in a given environment, or habitat patch, to overall fitness of the parent depends on having offspring that perform the best in each environment. Under soft selection, all patches that offspring colonize contribute to parental fitness, so the proportion of offspring contributed to the next generation is proportional to the frequency of the different patches in the population (Lechowicz and Bell 1991, Kelley et al. 2005). Under this scenario, relative fitness of offspring from parents reared in different environments should be estimated by comparing the fitness of offspring within each offspring environment only. To do this, the fitness value of each parent is re-calculated relative to the mean, or the maximum, fitness found within each offspring environment.

If density-dependent mortality of offspring occurs at a spatial scale containing multiple habitat patches, followed by offspring dispersal to a range of different environments, where environment-specific selection then acts on offspring phenotypes, selection is said to be frequency-independent ('hard' selection; Dempster 1955). Because density-dependent mortality is 'global' and occurs

before environment-specific selection, offspring in the environment with the highest overall performance (i.e. high quality environments) contribute the most to parental fitness, regardless of the frequency of different environments (Gomulkiewicz and Kirkpatrick 1992). Under this scenario, absolute offspring fitness should be estimated by comparing the fitness of offspring from different parents among each offspring environment.

Therefore, mothers influencing their offspring to achieve high absolute fitness in the best offspring environment are favored under 'hard' selection, whereas mothers influencing their offspring to achieve relatively higher fitness within each environment are favored under 'soft' selection. Consequently, inferences from absolute versus relative fitness make different assumptions about how population density and the frequency of offspring environments in space affect the outcome of selection and its consequences to parental fitness. Evolutionary biologists have long been aware of the different evolutionary interpretations of absolute versus relative fitness (Lechowicz and Bell 1991, Kelley et al. 2005, Stanton and Thiede 2005, Orr 2009), but studies on parental effects usually draw inferences from only the absolute fitness benefits of a particular parental effect (cf. Burgess and Marshall 2011). The consequences of inappropriately focusing on relative or absolute fitness are nontrivial; as Stanton and Thiede (2005) demonstrate in their excellent consideration of this issue with regards to phenotypic plasticity, using the 'wrong' fitness measure can change estimates of how phenotypic variance is partitioned into genetic and environmental sources and thereby evolutionary trajectories of traits in a population.

#### ***Dispersal as an adaptation***

Rather than producing offspring with the highest performance in a given environment, APE's may also manifest as increases in dispersal. For example, when cues indicate to parents that local conditions are deteriorating (e.g. from increased competition or predator abundance), parents may produce more dispersive offspring to reduce the exposure of offspring to predictably poor local conditions (Weisser et al. 1999, Allen et al. 2008, Marshall 2008, Marshall and Keough 2009). By producing more dispersive offspring (e.g. winged morphs of aphids, Sutherland 1969, Weisser et al. 1999), individuals have the ability to disperse to other locations where the agent of selection on offspring phenotypes is weaker or absent (Weisser et al. 1999). Even under this situation however, APE's to increase dispersal propensity are only likely to evolve if there is temporal autocorrelation in local predation risk (Poethke et al. 2010), as well as spatial variation, underscoring the importance of quantifying environmental predictability.

#### ***Whose fitness is it – parents or offspring?***

Parental effects affect the fitness of both parents and offspring, but offspring fitness is typically assigned to the parent (Wolf and Wade 2001, Wilson et al. 2005, Marshall and Uller 2007). Assigning offspring fitness as a component of parental fitness raises some complications that need to be resolved for the purpose of evolutionary analysis. In particular, if offspring performance is determined by some combination of the parental genotype and the offspring genotype,

then assigning offspring fitness to parents affects how selection acts on the parental traits in two ways (Wolf and Wade 2001). Using a quantitative genetic model and assuming no environmental covariances between traits or across generations, no genotype–environment covariances, and linear selection Wolf and Wade (2001) (Eq. 5, 10, and A8 from Wolf and Wade 2001; an empirical example is given in Wilson et al. 2005) showed that: 1) assigning offspring fitness to the mother, as opposed to the offspring, can result in overestimating selection on the maternal trait if the environmental effects on the maternal trait do not affect the offspring phenotype, and 2) assigning offspring fitness to the mother can under-estimate the importance of viability selection on an individual's own value of the offspring trait before itself eventually becomes a mother. Assigning offspring fitness to the mother versus the offspring only yields the same expression for selection on a maternal trait when all of the phenotypic variance is determined by additive genetic variance and when there is no genetic covariance between the maternal trait and the offspring trait (i.e. when genes influencing the maternal trait do not also influence offspring fitness). Both of these conditions are unlikely such that assigning fitness to mothers or offspring carries significant risks. The analysis by Wolf and Wade highlights the importance of having an a priori understanding of the causal factors that influence parental and offspring fitness to understand how selection acts on traits related to APE's and how such traits evolve. Unfortunately, for most organisms, including the ones that we as authors have studied in the past, we have few or no estimates of these essential parameters and so are assigning fitness to mothers in the absence of a sound theoretical justification for doing so. While the experimental designs required to address the issues raised by Wolf and Wade (2001) are onerous (Wilson et al. 2005), we regard them as an important next step in understanding the evolutionary ecology of parental effects.

## Conclusion

A key but largely overlooked point in studies on APE's is that APE's will only be favored if the state of the parental environment is a good predictor of the state of the offspring environment in space or time (Marshall and Uller 2007). Studies that do not explicitly consider environmental predictability risk searching for APE's under circumstances where they are unlikely to occur. We believe this failure to quantify environmental predictability is widespread in the literature and is one of the major reasons for mixed evidence generated by some APE studies reported in Uller et al. (2013). We have provided an introduction to the methods evolutionary ecologists can use to quantify how predictable offspring environments are from parental environments, as well as some issues in measuring offspring fitness appropriately, in the hope that future studies will be able to more rigorously assess the importance of APE's. Such rigor is especially important given the increasing interest of ecologists in studying how the effects of transgenerational plasticity might mediate the biological consequences of climate change (Mondor et al. 2004, Miller et al. 2012, Salinas and Munch 2012).

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## References

- Agrawal, A. A. 2002. Herbivory and maternal effects: mechanisms and consequences of transgenerational induced plant resistance. – *Ecology* 83: 3408–3415.
- Agrawal, A. A. et al. 1999. Transgenerational induction of defences in animals and plants. – *Nature* 401: 60–63.
- Alekseev, V. and Lampert, W. 2001. Maternal control of resting-egg production in *Daphnia*. – *Nature* 414: 899–901.
- Allen, R. et al. 2008. Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. – *Am. Nat.* 171: 225–237.
- Badyaev, A. V and Uller, T. 2009. Parental effects in ecology and evolution: mechanisms, processes and implications. – *Phil. Trans. R. Soc. B* 364: 1169–1177.
- Benton, T. G. et al. 2001. Maternal effects and the stability of population dynamics in noisy environments. – *J. Anim. Ecol.* 70: 590–599.
- Benton, T. G. et al. 2005. Changes in maternal investment in eggs can affect population dynamics. – *Proc. R. Soc. B* 272: 1351–1356.
- Bonduriansky, R. and Day, T. 2009. Nongenetic inheritance and its evolutionary implications. – *Annu. Rev. Ecol. Evol. Syst.* 40: 103–125.
- Burgess, S. C. and Marshall, D. J. 2011. Temperature-induced maternal effects and environmental predictability. – *J. Exp. Biol.* 214: 2329–2336.
- Chevin, L. M. and Lande, R. 2010. When do adaptive plasticity and genetic evolution prevent extinction of a density-regulated population? – *Evolution*. 64: 1143–1150.
- Colwell, R. K. 1974. Predictability, constancy and contingency of periodic phenomena. – *Ecology* 55: 1148–1153.
- Crean, A. J. et al. 2013. Adaptive paternal effects? Experimental evidence that the paternal environment affects offspring performance. – *Ecology* 94: 2575–2582.
- Cuddington, K. M. and Yodzis, P. 1999. Black noise and population persistence. – *Proc. R. Soc. B* 266: 969–973.
- Dempster, E. 1955. Maintenance of heterogeneity. – *Cold Spring Harb. Symp. Quant. Biol. Sci.* 20: 25–32.
- DeWitt, T. J. et al. 1998. Costs and limits of phenotypic plasticity. – *Trends Ecol. Evol.* 13: 77–81.
- Donald-Matasci, M. et al. 2013. When unreliable cues are good enough. – *Am. Nat.* 182: 313–327.
- Donohue, K. and Schmitt, J. 1998. Maternal environmental effects in plants – adaptive plasticity? – In: Mousseau, T. A. and Fox, C. W. (eds), *Maternal effects as adaptations*, Oxford Univ. Press, . pp. 137–158.
- Dwyer, J. M. et al. 2010. Neighbourhood effects influence drought-induced mortality of savanna trees in Australia. – *J. Veg. Sci.* 21: 573–585.
- Einum, S. and Fleming, I. A. 2004. Environmental unpredictability and offspring size: conservative versus diversified bet-hedging. – *Evol. Ecol. Res.* 6: 443–455.
- Ezard, T. H. G. et al. The fitness costs of adaptation via phenotypic plasticity and maternal effects. – *Funct. Ecol. in press.* doi: 10.1111/1365-2435.12207
- Fischer, B. et al. 2010. How to balance the offspring quality-quantity tradeoff when environmental cues are unreliable. – *Oikos* 120: 258–270.
- Fox, C. W. et al. 1997. Egg size plasticity in a seed beetle: an adaptive maternal effect. – *Am. Nat.* 149: 149–163.

- Galloway, L. F. 2005. Maternal effects provide phenotypic adaptation to local environmental conditions. – *New Phytol.* 166: 93–99.
- Galloway, L. F. and Etterson, J. R. 2007. Transgenerational plasticity is adaptive in the wild. – *Science* 318: 1134–1136.
- Gomulkiewicz, R. and Kirkpatrick, M. 1992. Quantitative genetics and the evolution of reaction norms. – *Evolution*. 46: 390–411.
- Halley, J. M. 1996. Ecology, evolution and 1/f-noise. – *Trends Ecol. Evol.* 11: 33–37.
- Jensen, N. et al. Adaptive maternal and paternal effects: gamete plasticity in response to parental stress. – *Funct. Ecol.* in press. doi: 10.1111/1365-2435.12195
- Kaplan, R. H. 1992. Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis*. – *Ecology* 73: 280–288.
- Kelley, J. L. et al. 2005. Soft and hard selection on plant defence traits in *Arabidopsis thaliana*. – *Evol. Ecol. Res.* 7: 287–302.
- Kirkpatrick, M. and Lande, R. 1989. The evolution of maternal characters. – *Evolution*. 43: 485–503.
- Lechowicz, M. J. and Bell, G. 1991. The ecology and genetics of fitness in forest plants. 2. Microspatial heterogeneity of the edaphic environment. – *J. Ecol.* 79: 687–696.
- Legendre, P. and Legendre, L. 1998. Numerical ecology. – Elsevier.
- Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. – *Am. Nat.* 87: 331–333.
- Levins, R. 1968. Evolution in changing environments: some theoretical explorations. – Princeton Univ. Press.
- Marshall, D. J. 2008. Transgenerational plasticity in the sea: context-dependent maternal effects across the life history. – *Ecology* 89: 418–427.
- Marshall, D. J. and Uller, T. 2007. When is a maternal effect adaptive? – *Oikos* 116: 1957–1963.
- Marshall, D. J. and Keough, M. J. 2009. Does interspecific competition affect offspring provisioning. – *Ecology* 90: 487–495.
- Marshall, D. J. et al. 2008. Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. – *Ecology* 89: 2506–2517.
- Miller, G. M. et al. 2012. Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. – *Nat. Clim. Chang.* 2: 1–4.
- Mondor, E. B. et al. 2004. Transgenerational phenotypic plasticity under future atmospheric conditions. – *Ecol. Lett.* 7: 941–946.
- Mousseau, T. and Fox, C. W. 1998. Maternal effects as adaptations. – Oxford Univ. Press.
- Munday, P. L. et al. 2013. Predicting evolutionary responses to climate change in the sea. – *Ecol. Lett.* 16: 1488–1500.
- Orr, H. A. 2009. Fitness and its role in evolutionary genetics. – *Nat. Rev. Genet.* 10: 531–539.
- Parker, L. M. et al. 2009. The effect of ocean acidification and temperature on the fertilization and embryonic development of the Sydney rock oyster *Saccostrea glomerata* (Gould 1850). – *Global Change Biol.* 15: 2123–2136.
- Pinheiro, J. C. and Bates, D. M. 2000. Mixed-effects models in S and S-Plus. – Springer.
- Plaistow, S. J. et al. 2006. Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. – *Am. Nat.* 167: 206–215.
- Poethke, H. J. et al. 2010. Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. – *Am. Nat.* 175: 577–586.
- Ripa, J. and Lundberg, P. 1996. Noise colour and the risk of population extinctions. – *Proc. R. Soc. B* 263: 1751–1753.
- Ruokolainen, L. et al. 2009. Ecological and evolutionary dynamics under coloured environmental variation. – *Trends Ecol. Evol.* 24: 555–563.
- Sakai, A. K. and Oden, N. L. 1983. Spatial pattern of sex expression in silver maple (*Acer saccharinum* L.) – Morisita index and spatial auto-correlation. – *Am. Nat.* 122: 489–508.
- Salinas, S. and Munch, S. B. 2012. Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. – *Ecol. Lett.* 15: 159–163.
- Scheiner, S. M. and Holt, R. D. 2012. The genetics of phenotypic plasticity. X. Variation versus uncertainty. – *Ecol. Evol.* 2: 751–67.
- Stanton, M. L. and Thiede, D. A. 2005. Statistical convenience vs biological insight: consequences of data transformation for the analysis of fitness variation in heterogeneous environments. – *New Phytol.* 166: 319–337.
- Stearns, S. C. 1981. On measuring fluctuating environments: predictability, constancy and contingency. – *Ecology* 62: 185–199.
- Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.
- Sugihara, G. et al. 2012. Detecting causality in complex ecosystems. – *Science* 338 : 496–500.
- Sutherland, O. 1969. The role of crowding in the production of winged forms by two strains of the pea aphid, *Acyrtosiphon pisum*. – *J. Insect Physiol.* 15: 1385–1410.
- Torrence, C. and Compo, G. P. 1998. A practical guide to wavelet analysis. – *Bull. Am. Meteorol. Soc.* 79: 61–78.
- Trussell, G. C. et al. 2003. Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. – *Ecology* 84: 629–640.
- Uller, T. 2008. Developmental plasticity and the evolution of parental effects. – *Trends Ecol. Evol.* 23: 432–438.
- Uller, T. et al. 2013. Weak evidence for anticipatory parental effects in plants and animals. – *J. Evol. Biol.* 26: 2161–2170.
- van Tienderen, P. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. – *Evolution*. 45: 1317–1331.
- Vasseur, D. A. and Yodzis, P. 2004. The color of environmental noise. – *Ecology* 85: 1146–1152.
- Wallace, B. 1975. Hard and soft selection revisited. – *Evolution* 29: 465–473.
- Weisser, W. W. et al. 1999. Predator-induced morphological shift in the pea aphid. – *Proc. R. Soc. B* 266: 1175–1182.
- Wilson, A. J. et al. 2005. Selection on mothers and offspring: whose phenotype is it and does it matter? – *Evolution* 59: 451–463.
- Wolf, J. B. and Wade, M. J. 2001. On the assignment of fitness to parents and offspring: whose fitness is it and when does it matter? – *J. Evol. Biol.* 14: 347–356.
- Wolf, J. B. and Wade, M. J. 2009. What are maternal effects (and what are they not)? – *Phil. Trans. R. Soc. B* 364: 1107–1115.