When is a maternal effect adaptive?

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Maternal effects have become an important field of study in evolutionary ecology and there is an ongoing debate regarding their adaptive significance. Some maternal effects can act to increase offspring fitness and are called 'adaptive maternal effects'. However, other maternal effects decrease offspring fitness and there is confusion regarding whether certain maternal effects are indeed adaptive or merely physiological inevitabilities. Here we suggest that the focus on the consequences of maternal effects for offspring fitness only and the use of 'snapshot' estimates of fitness have misdirected our effort to understand the evolution of maternal effects. We suggest that selection typically acts on maternal effects to maximise maternal rather than (or in addition to) offspring fitness. We highlight the importance of considering how maternal effects influence maternal fitness across a mother's lifetime and describe four broad types of maternal effects using an outcome-based approach. Overall, we suggest that many maternal effects will have an adaptive basis for mothers, regardless of whether these effects increase or decrease survival or reproductive success of individual offspring.

Maternal effects occur when the phenotype of the mother or the environment she experiences influence the phenotype of her offspring over and above the direct effect of transmitted genes. Whilst maternal effects were originally considered troublesome sources of variation in quantitative genetic studies (Falconer 1981), evolutionary ecologists now recognise maternal effects as one of the most important influences on offspring pheno-type (Bernardo 1996a, Mousseau and Fox 1998, Wade 1998). For example, a number of studies have shown that mothers can match the phenotype of their off-spring to changes in the local environment and that maternal effects can be an effective means of buffering offspring from environmental stressors (Mousseau and Dingle 1991, Galloway 1995, Agrawal et al. 1999, Agrawal 2002). However, maternal effects can also decrease offspring fitness and act as a conduit by which environmental degradation in the maternal generation can decrease offspring performance (Bernardo 1996a, 1996b, Kofman 2002, McCormick 2006). This raises some fundamental questions: Why are some changes in the environment more likely to elicit a maternal effect than others? Why do some mothers react to environ-mental change by increasing offspring quality but other

mothers react by decreasing offspring quality? Whilst significant progress has been made in determining the importance of maternal effects and the numerous ways in which they can manifest, we believe we currently lack a conceptual framework that explicitly links environ-mental variation, maternal selection and offspring selection.

When local conditions change, maternal effects can act to increase offspring fitness in the subsequent generation. As such, maternal effects are often viewed as a form of adaptive, transgenerational plasticity and are sometimes termed 'adaptive maternal effects' (Ber-nardo 1996a, 1996b, Mousseau and Fox 1998, Agrawal 2001). However, several reviews express reservations regarding whether maternal effects are adaptive and indeed there are numerous examples of maternal effects decreasing offspring fitness (reviewed in Bernardo 1996a, 1996b, Rossiter 1996, Mayhew 2001, Kofman 2002, Groothuis et al. 2005). In such instances, maternal effects are often viewed as a simple conduit by which environmental variation passes through the maternal phenotype into the second generation. Furthermore, it has been suggested that some maternal effects (for example variation in offspring size within a

brood, or a maternal size-body size correlation) have no adaptive value and are more likely to be physiological side effects (Heath and Blouw 1998, Fox and Czesak 2000). Thus there has been continued debate on the adaptive significance of maternal effects (Heath and Blouw 1998, Mayhew 2001, Groothuis et al. 2005). We suggest that this debate has been hampered by three problems: 1) an inappropriate focus on offspring fitness; 2) an inappropriate time scale of observation; and 3) the use of single offspring traits/environments to estimate fitness.

Offspring vs maternal fitness

Currently, it appears that maternal effects are regarded as 'adaptive' on the basis of the consequences for offspring fitness (Mousseau and Fox 1998). However, a maternal effect can be regarded as a 'shared phenotype' that affects both maternal and offspring fitness simultaneously. For example, offspring size is both a phenotype of the offspring and the mother (Bernardo 1996b). Importantly, whilst maternal effects affect the fitness of both, selection will typically maximise maternal, rather than offspring fitness, particularly in species with no post-natal maternal care where the evolution of offspring counter-strategies may be less likely to evolve (Smith and Fretwell 1974, Trivers 1974, Bernardo 1996a, Marshall et al. 2006). Consider selection on offspring size: if selection acted to maximise offspring fitness, then mothers would produce a single, very large offspring (Bernardo 1996a). However, because selection acts to maximise maternal fitness, mothers tend to make smaller, more numerous offspring, effectively sacrificing individual offspring fitness for maternal fitness (Einum and Fleming 2000). Thus, mothers can achieve fitness gains by producing offspring that do not have the highest fitness possible. In other words, maternal and offspring fitness are not always correlated – mothers producing many offspring with poor fitness can have higher fitness than mothers that produce few offspring with high fitness. Overall then, focusing on the fitness consequences of maternal effects for offspring only is an inappropriate framework for considering whether a maternal effect is 'adaptive', and under most circumstances, a maternal focus is more appropriate (although parent-offspring conflict can affect the evolution of maternal effects if offspring can evolve counter-strategies to maternal strategies; Parker et al. 2002, offspring rarely completely control maternal allocation suggesting that the consequences of maternal effects for maternal fitness must always be taken into account). We suspect that many maternal effects are indeed strategies that have been selected for because they increase maternal fitness at the expense of offspring fitness. Critically, this assumes that a decrease in per

offspring maternal investment increases maternal reproductive success in that or a later reproductive bout. This leads us to our second point: the importance temporal scales at which maternal effects are observed.

Observing maternal effects through time

When one observes a maternal effect that decreases offspring fitness in a single reproductive bout, it is tempting to view it as having a negative influence on maternal fitness. However, the overall influence of a maternal effect on a subset of offspring can only be assessed in the context of life-time reproductive outputs. For example, when *Bugula neritina* bryozoan colonies experience a predation event, they produce smaller, less fit offspring immediately afterwards (Marshall and Keough 2004a). However, producing smaller offspring allows mothers to redirect resources away from reproduction and into recovery from predation, thereby increasing reproductive success in the future (Marshall and Keough 2004a). Similarly, younger earth mite mothers produce smaller (less fit) offspring but as they age, they produce larger, better provisioned offspring (Plaistow et al. 2007). This is because offspring born to older mothers will face higher levels of intraspecific competition from siblings and therefore require more resources in order to compete (Plaistow et al. 2007). Thus a short-term decrease in offspring fitness may result in longer term increase in maternal fitness. Overall then, it is crucial to examine the fitness consequences of a maternal effect across the entire reproductive life-span of the mother before making conclusions regarding its adaptive nature.

The influence of maternal effects across traits and environments

Maternal effects affect more than one aspect of offspring phenotype and their effects will typically be context-dependent (Rossiter 1996). However, most studies of maternal effects examine single offspring traits and typically examine only one environment. Whilst this is understandable from a logistical perspective, recent evidence highlights the fact that examining single traits or environments can cause an incomplete or even misleading view of the influence of maternal effects. For example, work in soil mites has shown that offspring provisioning can increase some components of offspring fitness but decrease others (Benton et al. 2005). Similarly, Dibattista et al. (2007) showed that larger offspring may have higher initial growth but are more likely to suffer predation. More generally, maternal effects are likely to affect a range of traits

simultaneously and these traits may tradeoff against each other suggesting that caution should be exercised when interpreting the consequences of a maternal effect on offspring fitness.

Not only can maternal effects affect a range of traits simultaneously, they are also likely to highly context-dependent. Numerous studies have shown that the relative strength and even direction of maternal effects can depend on local environmental conditions (Kaplan 1992, Einum and Fleming 1999, Fox 2000, Marshall and Keough 2004b, Plaistow et al. 2006). For example, Marshall (in press) showed that mothers exposed to a pollutant produced offspring that were more pollution resistant themselves. However, when offspring performance in the presence of competition and the absence of pollution was examined, the pollution resistant offspring performed more poorly (Marshall in press). Not only can local conditions determine the influence of maternal effects, the local conditions can also change dramatically over biologically relevant temporal and spatial scales (Marshall and Keough 2006, Plaistow et al. 2007). Thus the influence of maternal effects is likely to be highly dynamic and caution should be exercised when interpreting the importance or role of a maternal effect for a single trait or set of environmental conditions (see also below).

Classifying maternal effects

In the previous section we highlight the potential pitfalls when viewing maternal effects and classifying them as 'adaptive' or not. In this section we suggest an alternative, outcome-based approach to classifying different maternal effects that are commonly observed. By focusing on the consequences of maternal effects, our hope is that their evolutionary and demographic implications will become clearer.

Anticipatory maternal effects: increase maternal fitness by increasing offspring fitness

There is a growing list of studies across a range of taxa that show that mothers adjust the phenotype of their offspring according to local conditions so as to maximise offspring fitness (Fox et al. 1997, Agrawal et al. 1999, Agrawal 2001, 2002, Galloway 2001, Kudo and Nakahira 2005). In an excellent example in seed beetles, Fox and colleagues showed that mothers produce larger eggs when they lay on thick coated seeds: the extra resources allow offspring to bore through the thicker seed coats, thereby enhancing offspring (and therefore maternal) fitness (Fox et al.

1997, 1999). Similarly, in both animals and plants, mothers that are exposed to natural enemies produce offspring with a more resistant phenotype (Agrawal et al. 1999). If local conditions degrade, mothers can produce more dispersive offspring that are more likely to colonise better habitats (Sutherland 1969, Krug and Zimmer 2000, Allen et al. in press). If competition increases, mothers can produce larger, more competitive offspring (Plaistow et al. 2007, Allen et al. in press). It is typically this suite of maternal effects that are regarded as adaptive transgenerational phenotypic plasticity and, indeed, when the environment varies across generations, this form of plasticity can increase offspring (and thus maternal) fitness (Mousseau and Fox 1998). Models of phenotypic plasticity generally agree that plasticity is favored when (1) there is environmental heterogeneity (spatial or temporal), (2) there are cues that reliably predict future environmental conditions, and (3) the cost of plasticity is low (Berrigan and Scheiner 2004). Applied to the context of maternal effects, this suggest that maternally-induced phenotypic plasticity is favored when (1) environmental conditions can change between generations (i.e. temporal heterogeneity or among-generation spatial heterogeneity, e.g. due to dispersal), (2) offspring environmental conditions are predictable from maternal environmental conditions or maternal phenotype, (3) the costs of maternal cue detection and transmission of information or resources are low, and additionally that (4) the level of parent-offspring conflict is low (for an excellent description of the constraints and limits of phenotypic plasticity, DeWitt et al. 1998). Thus mothers must be able to 'anticipate' (or influence: Einum and Fleming 2002) the natal environment in order for mothers to produce offspring with the appropriate phenotype. We suggest that the term 'Anticipatory maternal effects' (AME's) be used to identify maternal effects which act to increase offspring fitness under spatial or temporal heterogeneity. Note that we recognise that this does not involve a conscious prediction regarding the offspring environment whereby mothers choose the appropriate phenotype of their offspring: rather we use the word 'anticipate' as a convenient shorthand to denote that selection should favour mothers that produce offspring of a certain phenotype when the maternal environment is a good predictor of the environment the offspring will encounter. By this definition, AME's should act to increase maternal fitness by increasing the fitness of offspring.

Importantly, as AME's constitute a form of phenotypic plasticity, a crucial prediction is that offspring from mothers anticipating environment A will do better in environment A than offspring from mothers anticipating environment B and vice versa. Thus, an appropriate test of whether a maternal effect has evolved as a means of adaptive transgenerational

plasticity requires a factorial experiment in which both maternal and offspring environments are manipulated. Although this approach is commonly employed for some maternal effects (Marshall in press), it has not yet been fully implemented for others.

Selfish maternal effects: increase maternal fitness at the expense of offspring fitness

Whilst a reduction in the quality of the local environment can result in mothers increasing the quality or performance of their offspring as described above, other changes in the maternal environment can lead to a reduction in the performance or quality of offspring that are produced (Scheirs et al. 2000, Sockman and Schwabl 2000, McCormick 2006). For example, ovipositing insect mothers that accumulate many unlaid eggs can often deposit their eggs on suboptimal plant hosts (Singer et al. 1992, Mayhew 2001, West and Cunningham 2002), and mothers that mate with lower quality males may reduce the quality (size) of their offspring (Cunningham and Russell 2000, Uller et al. 2005). Why do these maternal environments (or phenotypes) result in offspring that are likely to have poorer performance whereas others result in AME's? We suggest that selection on mothers can lead to maternal effects that reduce offspring fitness when: 1) the maternal effect is costly to the mother, 2) mothers are capable of reproducing repeatedly (i.e. creating conflicting selection pressures), 3) mothers have a chance of reproducing under 'better' conditions (i.e. the predicted returns on investment from future reproduction is high), or 4) selection on offspring strategies that reduce the negative maternal effect is inefficient (e.g. because of constraints; Uller et al. 2007).

The first of these conditions hold true for many, if not most, maternally induced changes in offspring quality or performance (via increases in offspring size, maternal care, or 'rescuing' the offspring phenotype: Bernardo 1996a). For example, increasing average propagule size incurs a fecundity cost in either the immediate or subsequent rounds of reproduction (Smith and Fretwell 1974). Similarly, continuing to search for high quality host plants when insect mothers carry a high egg load carries a number of direct and indirect costs that may decrease the long term fitness of mothers (Fletcher et al. 1994, Mayhew 2001). Thus increasing maternal investment typically incurs a cost on mothers that will reduce either current or future fecundity. Therefore, the potential exists for mothers to gain long term fitness benefits by decreasing their investment. Ultimately, the fitness benefits of decreasing current per offspring investment depend on the relationship between maternal investment and offspring fitness (for a detailed consideration of the long term tradeoffs of maternal effects, Livnat et al. 2005). Alternatively, if conditions are very challenging for maternal survival, mothers may ensure their own survival by reducing the quality of their offspring (e.g. via termination of parental care; Marshall and Keough 2004a). Under both scenarios described above, mothers should achieve higher fitness overall by trading offspring quality for quantity (although when the maternal effect arises from resource transfer, mothers may simply make fewer offspring). Mothers utilising this strategy could be termed 'selfish' in that they maximise their overall fitness at the expense of their current offsprings' chances of survival and thus we suggest the term Selfish maternal effects (SME's) for examples such as these. Under this definition, brood reduction in birds (Stenning 1996) and brood cannibalism in amphipods (Sheader 1983) would represent the most extreme form of SME's.

Bet-hedging maternal effects: reduce variance in maternal fitness by producing offspring with a range of phenotypes

Adjusting the mean quality/phenotype of offspring is not the only way in which mothers may increase their overall fitness. For one set of environmental conditions, one phenotype will typically have higher fitness than most others and so any deviation from that phenotype will result in decreased offspring fitness. Thus mothers that produce offspring with a range of offspring phenotypes are producing some offspring that are likely to be less fit than others (Kudo 2001). However, under unpredictable temporal or spatial environmental heterogeneity (and consequently selective pressures), selection may favour mothers that produce a range of offspring phenotypes since this reduces the variance in her reproductive success and, consequently, maximizes the geometric mean fitness across breeding events (i.e. bet-hedging, Seger and Brockman 1987, Philippi and Seger 1989). For example, if mothers cannot 'predict' the habitat or competitive environment of their offspring, producing a range of offspring sizes rather than a single offspring size could be favoured (Capinera 1979, Crump 1981, McGinley et al. 1987, Geritz 1995, Dziminski and Alford 2005). Mothers can also manipulate the dispersal profiles of their offspring and, in a range of taxa, mothers produce offspring with a range of dispersal phenotypes so as to 'spread their risk' with regards to the colonisation of new habitats (Strathmann 1974, Zera and Denno 1997, Krug and Zimmer 2000, Krug 2001, Toonen and Pawlik 2001).

Similarly, hatching asynchrony in birds has been viewed as a bet-hedging strategy to spread risk in space and time: not all offspring hatch simultaneously such that at least some offspring experience high quality conditions (Laaksonen 2004). This third class of maternal effects in which mothers manipulate the variance in the phenotype of her offspring can be termed 'Bet-hedging maternal effects'. It is worth noting that we do not suggest all variation in offspring phenotype within a clutch represents a bet-hedging strategy but that at least some of this variation can have an adaptive basis.

Producing offspring of a range of phenotypes is termed diversified bet-hedging but it has been suggested that there is another form of bet-hedging, 'conservative bet-hedging', that mothers may employ in response to unpredictable environment. Einum and Fleming (2004) suggest that by producing very high quality offspring regardless of variation in environmental conditions, these offspring will survive and reproduce and that selection therefore would favour females that consistently produced high quality offspring. However, recent evidence suggests that conservative bet-hedging will only be favoured under specific conditions and that, under many circumstances, diversified bet-hedging is more likely (Marshall et al. unpubl.). Nevertheless, we agree with Einum and Fleming (2004) that conservative bet-hedging is likely in some instances and therefore distinguishing between AME's and a conservative bet-hedging strategy may be difficult as both may increase offspring fitness.

Transmissive maternal effects: reduction in both maternal and offspring fitness

In some instances, maternal effects benefit neither offspring nor parent and do not appear to fit into any of the above categories. For example, transmission of some pathogens from mother to offspring (Bernardo 1996a) or exposure to toxicants can produce offspring that have little or no potential to survive (Wiklund and Sundelin 2001). It is hard to envisage any adaptive basis for the transmission of such effects. We suggest that these type of maternal effects be classed as 'Transmissive maternal effects' (TME's) because environmental variation that affects the maternal phenotype is transmitted through to affect the offspring phenotype despite being selected against in both offspring and mother. It is difficult to generalise about the incidence of TME's but we predict that they are likely to occur due to pathogens that co-evolve with their hosts and are thereby adapted to be transmitted through generations despite the fact that such transmission may negatively affect the fitness of hosts (Rossiter 1996). Physiological constraints may also prevent buffering of maternally produced substances despite that the transmission (but not production) is selected against in both mothers and offspring (e.g. maternal hormones; Kofman 2002, Groothuis et al. 2005, Uller et al. 2007). Furthermore, novel (or at least, rare) compounds such as anthropogenic pollution are likely to elicit TME's if the organism has no experience of that pollutant (over evolutionary time) and therefore an adaptive response have not yet had the opportunity to evolve. For example, there are a number of comprehensive reviews on the effects of maternal exposure to toxicants on the subsequent phenotype of offspring in humans (Gallagher et al. 1998, Sram et al. 2005).

Conclusions

We have outlined some of the problems associated with interpreting different maternal effects as adaptive or not and presented some broad classes of maternal effects that are likely to be common in many taxa. Whilst we think it useful to view maternal effects in the above framework, we would discourage a static view of maternal effects and emphasise that maternal effects are highly dynamic and context-dependent such that they may change with shifts in maternal resources or natal environments and that different categories of maternal effects may interact. For example, in both bryozoans and soil mites, mothers may produce small, poor quality offspring when resources are scarce (i.e. sacrificing offspring quality for future reproduction – an SME) but when they are larger and they have accumulated more resources (due to the SME 'saving' resources), they produce larger, higher quality offspring that are better able to compete (an AME; Plaistow et al. 2007, Allen et al. in press). Ultimately, the nature of a maternal effect will depend on maternal resource state/ life-expectancy, environmental conditions (heterogeneity and predictability), parent-offspring conflict, constraints and the relationship between the costs of producing a certain offspring phenotype and benefits of that phenotype. We suggest that AME's, SME's and BME's are all likely to increase maternal fitness in some instances (i.e. be 'adaptive') but that, typically, only AME's will result in an increase in offspring fitness.

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