Developmental plasticity and the evolution of parental effects

Tobias Uller

Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

One of the outstanding challenges for evolutionary biologists is to understand how developmental plasticity can influence the evolutionary process. Developmental plasticity frequently involves parental effects, which might enable adaptive and context-dependent transgenerational transmission of phenotypic strategies. However, parent–offspring conflict will frequently result in parental effects that are suboptimal for parents, offspring or both. The fitness consequences of parental effects at evolutionary equilibrium will depend on how conflicts can be resolved by modifications of developmental processes, suggesting that proximate studies of development can inform ultimate questions. Furthermore, recent studies of plants and animals show how studies of parental effects in an ecological context provide important insights into the origin and evolution of adaptation under variable environmental conditions.

Developmental plasticity and parental effects

There is a growing awareness that evolutionary biologists need to redirect their focus away from a narrow gene-centered view and toward developmental aspects of phenotypic evolution, to fully understand the evolution of organismal form and function [1–6]. This change in focus requires us first to extend our view of heredity to include epigenetic inheritance [1–3] and second to address the role of developmental plasticity in initiating and directing adaptive evolution [4,5].

Together, the transmission of non-genetic developmental factors and developmental plasticity result in an effect of the parental phenotype on offspring phenotype that cannot solely be ascribed to inherited genes. Thus, parental effects [7] represent a form of plasticity that spans generations. Although parental effects initially received scant treatment by ecologists and evolutionary biologists, there has been a rapid accumulation of studies since a landmark publication 10 years ago [7]. This book has been instrumental for the general acceptance of parental (in particular maternal) effects as an important factor in evolution. However, many limitations to our understanding of evolution of parental effects still remain. For example, whereas theoretical work has focused on the consequences of parental effects for the short-term response of traits to selection [8–11], empirical studies tend mainly to be concerned with whether or not parental effects are adaptive [7,12–14]. Thus, it remains unclear under what circumstances parental effects are selected for, and the relative contribution of evolution of parental and offspring strategies [14,15].

This review attempts to take a step toward filling this gap by outlining a framework for the evolution of parental effects. It does so by integrating selection, parent–offspring conflict [16,17], developmental plasticity and proximate mechanisms of interactions between parents, offspring and their environments. Such an approach helps to clarify the circumstances that will select for the parental and offspring strategies that comprise parental effects, and to estimate their fitness consequences. Importantly, the approach also shows that understanding the evolution of parental effects requires knowledge both of the selection pressures involved and of the ways in which conflicts and constraints can be resolved.

Evolution when everyone agrees: adaptive transgenerational phenotypic plasticity

Parental effects represent a form of phenotypic plasticity spanning generations. Models of within-generation phenotypic plasticity generally predict that plasticity is favored when (i) there is environmental heterogeneity (spatial or temporal), (ii) there are cues that reliably predict future environmental conditions and, hence, selective regimes and (iii) the cost of plasticity is low [18,19]. Applied to the context of parental effects, this suggests that parentally induced plasticity is favored when (i) there is temporal or spatial fluctuation in environments across generations, (ii) offspring environmental conditions are predictable from the parental environmental conditions or the parental phenotype and (iii) the cost of obtaining information and responding appropriately is low for both parents and offspring. Furthermore, the level of parent–offspring conflict should be low, because otherwise the optimal level of plasticity will differ for parents and offspring.

Glossary

Development: phenotypic change during the lifetime of an individual.
Developmental plasticity: the ability of a genotype to give rise to multiple phenotypes in different environments.
Epigenetic inheritance: according to the broad definition, epigenetic inheritance means transgenerational transmission of form by other means than DNA. According to the narrow definition it implies inheritable variation in DNA expression or activity, for example via persistent DNA methylation.
Parent–offspring conflict: evolutionary conflict arising from different fitness optima in parents and offspring.
Parental effect: an effect of the parental phenotype on offspring phenotype that cannot solely be ascribed to the parental or offspring genome, non-parental components of the environment or the interaction between these.
Phenotypic plasticity: synonymous with developmental plasticity.
offspring and fitness might not be maximized for any of the individuals (see below).

The above criteria seem to apply to many taxa, and parental effects that increase the fitness of both offspring and parents have indeed been documented in both plants and animals (Boxes 1,2). However, across-generation heterogeneity and selection for developmental plasticity are not sufficient for parental effects to be favored. Cues to what constitutes optimal phenotypic development can be obtained by the offspring either through the parents or through other aspects of offspring environment. Thus, whether the parental phenotype will affect offspring development should also depend on the reliability of information provided by parents versus that obtained through the non-parental environment. Furthermore, parental effects will only be favored when there is a high likelihood that parental induction will allow an appropriate timing of the adaptive response in offspring (Box 1). For example, in plants and insects, lack of offspring sensory organs that can detect reliable cues early in development might explain why germination, diapause and dispersal strategies are commonly under maternal control, rather than being affected by environmental conditions experienced by the offspring [20,21].

Evolution of parental effects under parent–offspring conflict
Parental effects represent the outcome of interactions between parents and offspring. Thus, their evolution will be affected by selection pressures acting on both generations, and parent–offspring conflicts will occur whenever there are different optimal strategies for parents and offspring [16,17]. This means that selection on parents might favor parental effects that reduce offspring fitness [14,22]. By contrast, offspring are under selection to maximize their own fitness, not that of the parents [16]. Thus, the evolutionary dynamics of parent–offspring conflict will depend on the relative costs and benefits to the interacting individuals, the strength of selection and the potential for control. The fitness consequences of parental effects for parents and offspring reflect the evolutionary outcome of this conflict (i.e. who wins, and at what cost?) [16,17,23].

Costs and benefits of parental effects
The strength of selection on parental and offspring strategies depends on the costs and benefits involved. Many parental effects, such as investment in egg size or parental care, will reduce the future reproductive success of parents and therefore come at a cost. Other effects might entail minor costs for the parents, such as active or passive transmission of trace elements or hormones [13]. Parental effects can also entail costs for the offspring. For example, in birds, offspring have to compete for food by exhibiting costly behaviors, which reduces the amount of ingested food that can be directly converted to growth [23].

The costs of parental effects are important because they influence the level of parent–offspring conflict via the tradeoff between current and future reproductive success of parents, and because they offset the benefits of offspring strategies that manipulate parents. Thus, the evolutionary dynamics of parent–offspring interactions might differ depending on whether the parental effect involves costly investment or cheap manipulation.

Transmission of costly resources
When offspring cannot exercise any control over parental investment, parents might be able to impose their own optimal allocation to offspring within and between broods, despite negative effects on offspring [14]. For example, insect females do not always oviposit on hosts that are optimal for offspring development, but rather optimize maternal fitness via a tradeoff between search time and feeding time [22]. Similarly, females are expected to adjust
Box 2. Adaptive transgenerational plasticity in plants

Environments are frequently heterogeneous at the population level, with corresponding variation in phenotypic optima. Dispersal or active habitat choice might cause nonrandom associations between the environment experienced by parents and offspring. For example, in many species of plants, seed dispersal is limited, suggesting that the maternal environment provides cues about the selective pressure experienced by the offspring [14,21]. In some cases, this might lead to genetic assimilation of developmental plasticity and local adaptation at a small spatial scale [4,51]. However, when pollen dispersal occurs at significantly longer distances than does dispersal of seeds, the paternally inherited genotype does not provide accurate cues to optimal phenotypic development [12,52,53]. Thus, phenotypic plasticity in response to the local environment should be favored. One possible reason is that the offspring phenotype is modulated in response to the maternal environment, that is, a maternal effect on seedling development [12,21].

Recent studies of the herb *Campanulastrum americanum* (Figure I) have provided substantial evidence for a positive correlation between offspring and maternal, but not paternal, light conditions during growth [12]. Previous studies have shown that seeds from plants grown under good light conditions have an increased probability of germinating in the fall and, hence, of developing as an annual [54]. This might be adaptive if it increases population growth rate under favorable conditions. Indeed, a factorial field experiment [54] showed that seeds grown in the same environment as their mother had increased survival compared to seeds grown in the opposite environment. Furthermore, despite the fact that the maternal environment did not have a significant effect on adult fitness, the projected population growth was higher when environments were matched as a result of differential maternal effects on offspring survival and life history [54]. Parental effects on germination could be favored even in the face of occasional seed dispersal between habitats, as the negative effect will only persist in one generation. The documentation of adaptive transgenerational plasticity in this and other plants implies exciting opportunities for addressing the underlying mechanisms of transgenerational plasticity, and investigating to what extent such plasticity involves epigenetic programming that could span more than one generation [42,43].

![Figure I. Campanulastrum americanum. Picture by Laura Galloway.](image)

When offspring are able to influence the resource allocation of their parents, however, the evolutionarily stable parental effect might not reflect the parental optimum. Most theoretical work on parent–offspring conflict over negotiable resources (i.e. when both offspring and parents can respond to each others’ strategies) has been inspired by maternal or paternal food provisioning in birds and mammals [17,23]. However, several assumptions and predictions of the theory have also recently been put to the test using invertebrate systems with parental care [26,27], and the models might have broader applications. A common theoretical outcome of parent–offspring conflict over costly parental effects is that parents tend to provide more resources than is optimal for them [17]. The extent of the deviation from the parental optimum is set by the degree to which increased resource provisioning reduces (costly) offspring solicitation, and the degree to which solicitation affects parental provisioning [17,28], both of which can evolve. Empirical tests of whether the level of parental investment is at the parental or offspring optimum (or at neither) are hampered by the difficulty of measuring the parental fitness returns of variable resource provisioning to specific offspring or clutches, as both the returns from the current brood and returns from future broods need to be taken into account. Relatively novel model systems, such as burying beetles [26,27], might prove to be highly useful in this context.

Finally, parental effects might also be sensitive to conflicts over resource investment between parents [29,30]. This complicates the evolutionary dynamics and can even lead to the evolution of parent-of-origin effects on gene expression (i.e. genomic imprinting [31]). For example, when the paternal and offspring optimum of maternal investment is higher than that of the mother, and offspring can influence the amount of resource investment, genes that increase maternal provisioning when inherited paternally will be positively selected [31,32]. Indeed, imprinting seems to be most common in mammals, perhaps because of the high potential for offspring manipulation of maternal resource provisioning.

**Transmission of manipulative signals**

When parental effects are cost free in terms of parental acquisition, production and transmission of developmental factors, the evolutionary outcome can be very different...
from when they are costly to parents. Consider a parental strategy that can induce a plastic response in the offspring without any direct costs to the parents. One example might be hormone allocation to eggs or embryos [13, 33], but the argument should apply to any parental effect that does not compromise future reproductive success of parents. Selection can initially favor the use of manipulative signals, such as parental hormone allocation, even if it has an immediate negative effect on the fitness of individual offspring. For example, parents might use manipulative signals to mediate sibling conflict under asymmetric offspring competition by reducing the competitive ability of specific offspring within the brood, thereby increasing parental fitness [23]. Alternatively, selection can favor parental reinforcement of sibling competitive asymmetry to increase the likelihood of survival of the most valuable offspring or to reduce the cost of parental investment [17, 23]. However, selection on offspring will favor reduced offspring sensitivity or response to parental hormones, thereby generating an evolutionary arms race between parent and offspring. Evolutionary stability could be reached when offspring have lost the sensitivity to parental hormones altogether. Alternatively, the costs to parents might eventually outweigh the benefits, for example owing to negative pleiotropic effects of increased hormone levels on the physiology or behavior of parents [33]. Both conditions should result in a parental effect closer to the offspring optimum. On the contrary, there might be constraints on the ability of the offspring to ignore the parental manipulation, which would allow for an outcome closer to the parental optimum. For hormones, this could arise as a result of a necessity for offspring to be sensitive to their own, endogenous hormones required for normal development, which could be indistinguishable from those produced and transmitted by the parents [33, 34].

Selection on offspring will also favor the use of existing parental strategies according to the optimum of the offspring, not that of the parents. This might again lead to a parental effect close to the offspring optimum. However, selection on parents is then expected to reduce the transmission of information across generations, either via changes in the parental phenotype or via a temporal or spatial separation of generations (e.g., reduction in the duration of parental care), both of which reduce the availability of cues to offspring and lead to a reduction in the strength of the parental effects.

Although explicit models of parental effects are rare, the arguments outlined above question the validity of some proposed adaptive scenarios, whereby parents are suggested to be able to impose their own optima using manipulative signals (as has been suggested for hormone-mediated maternal effects [35]; see Ref. [33] for discussion). Furthermore, they might suggest that parental effects...
based on the transmission of manipulative signals are inherently unstable unless there are limits to evolutionary responses in parental manipulation or development of offspring counterstrategies. Such limits could arise from several types of constraint, including physical, genetic and developmental constraints. Thus, understanding the evolutionary dynamics of parental effects requires researchers to integrate proximate and ultimate levels of explanation [15] (Box 3).

Integrating proximate and ultimate levels of explanation in parental effects research

An evolutionary response to current selection requires that novel input or modification of responses can be incorporated into existing developmental systems. Thus, development might constrain or bias evolution [4,36]. Furthermore, theoretical models of parental effects under situations of conflict have shown that the outcome is sensitive to assumptions regarding the ability of parents and offspring to develop counterresponses to novel strategies exhibited by the other party, both at ontogenetic and evolutionary timescales [17,37]. Empirical studies of proximate mechanisms might therefore provide insights into ultimate questions by showing how such constraints can be resolved, in a way that maintains the fecundity and survival of parents (Box 3).

At the phenotypic level, parental effects are potentially sensitive to bias, limitations or constraints during several steps, from information acquisition by parents to the incorporation of developmental factors by offspring. For example, adaptive parental effects could be constrained owing to species-specific patterns of reproductive investment and parental care [15,54]. In mammals, the intimate physiological connection between mothers and offspring could make parental effects that are detrimental to offspring more likely by increasing the risk of negative carry-over effects of strategies favored by strong parental selection. For example, maternal strategies that ensure her survival during stress, including reduced resource provisioning to offspring or increased levels of circulating steroids [38], could have immediate negative effects on offspring of her current brood. This is particularly likely if there are constraints on evolutionary responses of offspring that allow them to cope with variation in maternal phenotype, which shows the importance of mechanistic studies of development to understand evolutionary outcomes [33]. Close physical or physiological association between parents and offspring also increases the risk that parental exposure to novel environments or substances, such as endocrine disruptors or pollutants, will also have negative effects on offspring (e.g. [39]).

Although parental effects generally are stronger early in life [7,40,41], they can have long-lasting consequences. This can be because of priming effects on phenotypic organization [4,38] or via lasting modification of gene expression via DNA methylation (i.e. epigenetic effects [1,42]). Intriguingly, studies on both plants and animals have shown that epigenetic effects not only remain stable within individuals, but also that they can be inherited across generations [1,39,42,43]. Thus, the presence of parental effects does not necessarily rely upon substantial contributions over and above genome transmission, suggesting that paternal effects might be more common than previously believed [44]. Furthermore, stable environmentally induced changes in gene expression provide a mechanism whereby short-term exposure to environmental conditions can have phenotypic consequences for more than two generations [1,42,43]. However, more transient parental effects can also have consequences for future generations, in particular if they affect mate preferences or sexual attractiveness of offspring (e.g. [45,46]). Documenting the proximate mechanisms of parental effects and their stability during transmission is therefore important to understand their adaptive value and to predict their effects on population dynamics.

Concluding remarks

The sheer number of studies of parental effects in virtually all major taxa is testimony to their importance. Furthermore, parental effects are fundamental to the ongoing integration of development, ecology and evolution [1–6], as they represent a particular form of plasticity arising from transmission of non-genetic developmental factors. To what extent parental effects involve permanent changes to gene expression [42,43] or only transient modifications of development remains poorly understood. However, if they are indeed stable, this could have far-reaching consequences for our understanding of the non-genetic transmission of form [1,42]. Progress in the field will require both the development of theoretical models that can be

---

**Box 4. Some challenges for the future**

**Theoretical**
- Extending models of within-generation plasticity to encompass transgenerational phenomena in systems with and without conflicts.
- Investigating the role of costs for both parents and offspring for the evolutionary dynamics of parental effects.
- Incorporating mechanistic assumptions to establish how constraints influence evolutionary outcomes.
- Addressing when epigenetic effects transmitted for more than one generation can be favored by selection.
- Developing models that link parental effects, population dynamics and evolution, for example, via parental effects on offspring attractiveness or reproductive output.
- Modeling the role of paternal effects during species invasions and its consequences for the rate and direction of evolution during colonization of novel habitats.

**Empirical**
- Putting models of the evolutionary outcome of parental effects with or without conflicts to the test in natural settings.
- Establishing comparative patterns of the strength and direction of parental effects for parental and offspring fitness in relation to key predictors, such as environmental heterogeneity and conflicting selection pressures.
- Using artificial selection experiments to tease apart the relative contribution of evolution of parental versus offspring strategies for the evolution of parental effects.
- Exploring mechanisms of parental effects and their consequences for evolutionary responses of parental and offspring strategies.
- Testing the stability of epigenetic inheritance across environmental contexts.
- Addressing how parental effects can affect population dynamics and facilitate range expansion or colonization of novel environments.
used to design and interpret empirical studies as well as explicit tests of adaptive scenarios in ecological settings (Box 4). Empirical tests of the adaptive value of parental effects are perhaps most promising in organisms such as plants where environmental heterogeneity often can be accurately described, conflicts are relatively weak or where there is limited scope for offspring manipulation of parental strategies [14,21]. Similarly, studies of egg or seed size are often freed from the potential for evolution of offspring counterstrategies, making those systems tractable for tests of adaptive scenarios. Parental effects arising from epigenetic modification via manipulative signals or cues in systems with conflicts are currently the least well understood. At the same time, they might provide some of the best opportunities for addressing the role of developmental plasticity and epigenetic inheritance for the origin and maintenance of complex adaptations more generally. Thus, the study of parental effects has the potential to become a prime example of how combining methods and concepts from different biological disciplines can lead to fundamental insights into evolutionary processes.

Acknowledgements
I am grateful to Alex Badyaev, Caroline Isaksson, Dustin Marshall, Geoff While and two anonymous reviewers for stimulating discussions and helpful suggestions on the manuscript. The Wenner-Gren Foundations and the Australian Research Council provided financial support.

References