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Introduction

Evolution of maternal effects: past and present

1. A BRIEF HISTORY OF 'MATERNAL EFFECTS AS ADAPTATIONS', 1998

It has been said that many original ideas reflect a convergence of related thought that coalesces into a unified representation of what many have been thinking. This is certainly true for the subfield of maternal effects evolution. The study of maternal effects has a long history. The first two papers reported in the ISI database dealing with the evolutionary significance of maternal effects were published in *Proceedings of the National Academy of Science USA* by Dobzhansky & Sturtevant (Dobzhansky 1935, 'Maternal effect as a cause of the difference between the reciprocal crosses in *Drosophila pseudoobscura*'; Dobzhansky & Sturtevant 1935, 'Further data on maternal effects in *Drosophila pseudoobscura* hybrids'). Surprisingly, given its authors, these papers have received little attention in the literature (a total of 12 citations for the Dobzhansky and Sturtevant paper), perhaps because of their relatively recent addition to electronically searchable databases, although the third paper in the list, by Walton & Hammond (1938), dealing with maternal effects in Shetland ponies, has been well cited (total of 228 citations) with an increasing rate of citation in the past decade. Overall, prior to 1987, ISI reports a total of 185 publications with 'maternal effects' as a keyword phrase. Between 1988 and 1997 this number jumped to 520 papers, while from 1998 to the present (November 2008) there have been at least 1397 publications on this topic. These numbers are underestimates, especially for the latter years, as they do not include the many keyword variants of relevant processes (e.g. maternal inheritance, maternal genetic effects, parental effects, epigenetic effects), or papers where the primary emphasis is in a different but related area, but they do reflect a dramatic increase in awareness following the late 1980s of the importance of maternal effects in the evolutionary process.

It has been 10 years since the publication of *Maternal effects as adaptations* by Oxford University Press (Mousseau & Fox 1998*a*). On a geological time scale this is barely measurable, but in the constantly evolving fields of biology, it is an aeon. This edited volume, and its companion paper in *Trends in Ecology and Evolution* (Mousseau & Fox 1998*b*), represented the culmination of a decade of excitement in the evolutionary community about the evolutionary significance of maternal effects that perhaps had its first big push with an *Annual Review of Ecology and Systematics* paper by Roach & Wulff (1987: 'Maternal effects in plants') and the seminal theoretical article in *Evolution* by Kirkpatrick & Lande (1989: 'The evolution of maternal characters'). Roach & Wulff (1987) were the first to empirically support the near-ubiquitous role of maternal effects in plant early development and life histories, while Kirkpatrick & Lande (1989) were the first to mathematically describe in approachable terms the potential for maternal effects to accelerate or deter evolutionary response to selection; they also demonstrated how maternal effects could generate sustained oscillations in trait response even after selection had stopped, a mysterious pattern observed in some mammal and insect populations. Collectively, these two papers truly inspired much of the modern excitement concerning the role of maternal effects in evolutionary biology and were key motivators for the organization of *Maternal effects as adaptations* (Mousseau & Fox 1998*a*).

However, the intellectual lineage leading to *Maternal effects as adaptation* was propelled primarily by the quantitative genetic explorations of transgenerational genetic and phenotypic interactions conducted by the late Bruce Riska, who at the time (the late 1980s) was a struggling postdoctoral fellow at the University of California, Davis, working under the mentorship of Michael Turelli, an expert in the field of evolutionary quantitative genetics. Riska, who was strongly influenced by his previous mentors (e.g. William Atchley, Tim Prout, Jim Rutledge, Bill Hill, Clark Cockerham and Gene Eisen), and by his contemporaries (e.g. Jim Cheverud, Barry Sinervo, Thomas Mitchell-Olds, Dave Cowley and Russ Lande), had been trying to quantify the many direct and indirect phenotypic and genetic contributions to individual phenotype that determine evolutionary response to selection. Riska's main contributions to this field were to integrate many of the previous statistical treatments of quantitative genetics, mainly derived from the agricultural and animal breeding literature, with contemporary evolutionary thought, which resulted in several landmark papers (e.g. Riska *et al.* 1984, 1985; Riska 1986, 1989). These papers influenced many subsequent papers in this field, and Bruce's insights concerning early development clearly pointed to the importance of the environment provided by mothers in shaping offspring phenotype, the target of selection in his models.

Bruce's enthusiasm for this topic led to a special symposium at the Fourth International Congress of Systematic and Evolutionary Biology (ICSEB IV) in 1990 at the University of Maryland which was subsequently published as a two volume edition, *The unity of evolutionary biology*, by Dioscorides Press

One contribution of 12 to a Theme Issue 'Evolution of parental effects: conceptual issues and empirical patterns'.

(Dudley 1991). Although not widely cited, this volume had a profound influence on the field of maternal effects evolution as it brought together for the first time many of the young scientists who were just getting started in evolutionary biology (e.g. Tim Mousseau, Barry Sinervo, Dave Cowley and Robert Kaplan). This symposium and its proceedings volumes directly or indirectly inspired several subsequent empirical and review papers (e.g. Mousseau & Dingle 1991; Bernardo 1996*a*,*b*; Rossiter 1996; Sinervo & Doughty 1996) that ultimately resulted in a second symposium in Bruce Riska's honour at the 1996 Society for the Study of Evolution (SSE) meetings in St Louis, which synergized the book, *Maternal effects as adaptations*.

In 1995, Tim Mousseau had several motivations to organize the SSE symposium and the associated edited volume. First, he felt obliged to continue the good work of Bruce Riska, who had been involved in a serious bicycle accident in 1990 and was thus not able to continue his work in this field. *Maternal effects as adaptations* really was inspired by his enthusiasm and mentorship while Tim was an NSERC (Canada) postdoctoral fellow with Hugh Dingle at UC Davis. Many of the contributors to the book share similar sentiments towards Bruce and his role in vitalizing the maternal effects wave of evolutionary biology. Second, at that time, Tim was looking for a special project on which to collaborate with Chuck Fox, then a postdoctoral fellow in the Mousseau lab at the University of South Carolina (now a professor at the University of Kentucky), who had been conducting exciting experimental work with beetles exploring the role of maternal effects and parental investment. Chuck subsequently made many important contributions to evolutionary biology and the study of maternal effects. Another coincident motivation for this project stemmed from Tim's undergoing a third year pre-tenure review as an assistant professor in 1994, knowing that tenure would require achievement of some measurable level of national recognition. An edited volume published by Oxford University Press seemed a good step in this direction!

Although it seems clear now that *Maternal effects as adaptations* played a significant role in promoting the study of maternal effects during the past decade (as evidenced by the many citations the contributors to this volume have received; the book itself has been cited more than 850 times), it is equally apparent that the time has come to account for the many significant new developments in this and related fields. With the advances of genomics, developmental biology and creative physiological manipulations, it seems very likely that many more discoveries are imminent concerning the role played by 'moms' in shaping offspring fitness. During the past two decades, we have learned that maternal effects can influence every imaginable target of selection in every organism that has been investigated and that many maternal effects have been shaped by natural selection to enable adaptive responses to heterogeneous environments. From the models of Riska, Kirkpatrick and Lande, to the empirical work highlighted in this theme issue, we now know that maternal effects can dramatically enhance rates of evolutionary response to selection in wild populations. It is now time to develop a comprehensive mechanistic understanding of how they work and are likely to evolve in the face of rapid environmental changes.

2. TEN YEARS LATER. EVOLUTION OF PARENTAL EFFECTS: CONCEPTUAL ISSUES AND EMPIRICAL PATTERNS

This theme issue grew from recognition that now—10 years after the landmark publication *Maternal effects as adaptations* (Mousseau & Fox 1998*a*)—is the time to bring together scientists with a common interest in the wider implications of maternal effects in order to provide a synthesis on the most important current research in ecology and evolution of maternal effects. Thus, in February 2008, Tobias Uller and Erik Wapstra organized a conference 'Evolution of parental effects: conceptual issues and empirical patterns' at the University of Wollongong, Australia that included presentations and discussion by researchers actively involved in the study of maternal effects, forming a foundation of this theme issue. That the time was right to revisit this rapidly growing field is evidenced by two more international conferences that, in 2008, marked 10 years of the publication of *Maternal effects as adaptations*: 'Maternal effects: underlying mechanisms and implications for life history evolution' in Adelboden, Switzerland in May and 'Maternal effects: evolution, physiology & implications for health and fitness' in the Association for the Study of Animal Behaviour Winter Meeting in London, UK in December.

The contributions presented here illustrate a diversity of current conceptual and empirical perspectives on the role of maternal effects in ecology and evolution. By linking mate choice and reproductive investment, maternal effects strongly affect sexual selection and evolution of breeding systems, and Harris & Uller (2009) capitalize on such dual influences to model the conditions under which mate quality results in differential resource allocation to offspring. Specifically, the authors distinguish between the hypotheses that predict greater maternal allocation to offspring produced with high-quality males (differential allocation) and those produced with low-quality males (reproductive compensation). Their results uncover both a crucial role of maternal effects in context-dependent reproductive decisions and the importance of female condition and mating opportunities for the evolution of mating strategies.

The importance of context dependence in the evolution of maternal effects is further elaborated by Plaistow & Benton (2009). They show that the extent to which maternal effects generate population cycles through delayed density dependence—a widely assumed pattern in population biology—depends on the expression of parental effects in a particular environment. They show experimentally that the contribution of maternal effects to population dynamics depends crucially on transient population density, the pattern attributed to context dependence of maternal effects at the level of individuals.

The important implication of this finding is that, in fluctuating populations, maternal effects do not always lead to sustained population cycles. Instead, maternal effects on population dynamics reflect context dependency of individual life histories, integrating present and past conditions of resource availability and parent–offspring transmission. The life-history perspective in the evolution of maternal effects is further emphasized by Donohue (2009), whose contribution focuses on the crucial role of maternal effects in maintaining dynamic life cycles. She examines maternal effects on annual plant germination and reviews laboratory and field studies examining the influence of maternal effects on phenology, demographic dynamics and genetic mechanisms behind life stage transitions in plants.

The notion that maternal effects link the environments experienced by parental and offspring generations and thereby enable continuity of life cycles is further explored by Duckworth (2009), who addresses a contribution of maternal effects to rapid range expansion and the evolution of colonization strategies. Duckworth uncovers important maternal effects on generation of variation in dispersal strategies in close association with resource availability—a finding that corroborates contributions of Donohue (2009) and Plaistow & Benton (2009) in establishing maternal effects as a bridge between maternal environment and offspring adaptations. The finding that under fluctuating environments maternal effects generate variance in offspring phenotypes that, in turn, enables evolution of local adaptations is further explored by Crean & Marshall (2009), who suggest that maternal effects on variation in offspring size within individual clutches is a bet-hedging strategy when the environment of offspring development is not predictable from the environment experienced by the maternal generation. An important implication of the finding that within-family variation in offspring size is a complex trait that reflects a compromise between selection pressures acting on maternal and offspring generations is echoed in the contribution by Brown & Shine (2009), who show that variation in offspring number has a direct phenotypic effect on offspring growth and size by determining the environment of offspring development. This finding has major implications for the evolution of life-history trade-offs and emphasizes the importance of explicitly considering the complexity of the developmental environment of offspring and the contribution of maternal effects to its construction.

That diverse phenomena and processes classified as maternal effects have distinct evolutionary and ecological dynamics is emphasized by Wolf & Wade (2009). The authors revisit the rationale for the quantitative genetics definition of maternal effects and stress that maternal effects operating at different levels of organization can have distinct evolutionary outcomes. The complex nature and diverse mechanisms behind maternal effects in ecology and their contribution to cyclic population dynamics are further explored by Inchausti & Ginzburg (2009), who show that conceptual development of the maternal effect hypothesis of population cycling has been greatly enriched by considerations of life-history trade-offs and individual quality in maternal effects on demographic composition of generations and corresponding population cycling.

The theme of maternal effects as a crucial component in continuity of life cycles is explored empirically by Badyaev (2009), who examines the role of maternal effects in the origin and evolution of novel adaptations that accompanied colonization of new environments by an invasive species. The author suggests that by connecting initial phenotypic accommodation of adaptive changes and their genetic inheritance, maternal effects represent a particularly clear illustration of the Baldwin effect—the process that links function and inheritance in the evolution of complex phenotypes. Russell & Lummaa (2009) further highlight that a careful consideration of processes underlying maternal effects in both maternal and offspring generations can clarify long-standing unresolved issues in biology. Specifically, the authors demonstrate that maternal effects have been neglected within cooperative breeding systems, despite their significant influences on reproductive and dispersal strategies. They further emphasize that overlooking maternal effects on reproductive decisions of offspring can lead to incorrect assignment of fitness in cooperative breeding strategies and thus impede understanding of their evolution. In the final contribution of the issue, Badyaev & Uller (2009) propose a novel conceptual framework that considers maternal effects as a stage in an evolutionary continuum—a composite entity that, capitalizing on the developmental offset between maternal and offspring generations, continuously accommodates and reconstructs the most reliable organism–environment configurations. The authors discuss the contribution of this framework to long-awaited unification of mechanisms behind the origination, modification and evolution of organismal diversity.

It is clear that the diversity of approaches, and interpretations and a breadth of scientific and taxonomic focus in this theme issue are indicative of a field undergoing explosive growth, but we also believe that a unified perspective on maternal effects in ecology and evolution is emerging—the perspective that might be strong enough to unite disparate research fields and approaches and to bring maternal effects to the forefront of the ongoing integration of development, ecology and evolution for another 10 years.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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