What is a paternal effect?

Angela J. Crean and Russell Bonduriansky

Evolution and Ecology Research Centre, and School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

Maternal effects are now universally recognised as a form of nongenetic parental influence on offspring but, until recently, paternal effects were regarded as an anomaly. Although it is now clear that paternal effects are both widespread and important, their proximate basis and evolutionary consequences have received little attention and remain poorly understood. In particular, because many paternal effects are mediated by maternal responses such as differential allocation, the boundary between paternal and maternal effects is sometimes blurred. We distinguish here three basic types of paternal effect and clarify the role of maternal responses in these effects. We also outline key questions that can serve as a road map for research on the proximate basis and evolutionary implications of paternal effects.

An unexpected source of heritable variation

Paternal effects (the influence of fathers on the features of their offspring via mechanisms other than the transmission of alleles) have long been regarded as a rare phenomenon confined to species exhibiting paternal care. However, a rapidly growing body of evidence now shows that such effects occur in a variety of organisms, can be mediated by cellular and physiological processes that characterise all sexually reproducing eukaryotic species, and affect a broad range of phenotypic traits in the next generation (reviewed in [1–5]).

The importance of paternal effects in evolutionary ecology derives from the fact that such effects represent a source of variation in phenotype and fitness. Theory suggests that paternal effects can have unique evolutionary consequences (e.g., [4,6,7]), and it is therefore important to identify paternal effects and distinguish them from other sources of variation. Nevertheless, whereas the nature and role of maternal effects has been examined by several authors [8–14], the distinct nature of paternal effects has received little consideration, and there is as yet no clear consensus on how paternal effects are to be defined, or differentiated from maternal effects. The lack of a clear framework for differentiating paternal effects from maternal effects is particularly evident in relation to a common class of paternal effects that are mediated by maternal responses. This is a potential source of confusion in many studies and, in particular, complicates the distinction between maternal differential allocation and paternal condition transfer.

We clarify here the definition of a paternal effect, distinguish several distinct routes of paternal influence on offspring, and show that paternal effects differ from maternal effects in fundamental ways. We also outline some key questions to guide research on paternal effects.

The nature of paternal effects

Parents contribute in many ways to the development of their offspring but, by conventional definition, a paternal (or maternal) effect can be said to occur when variation in the paternal (or maternal) genotype or phenotype is causally associated with variation in offspring phenotype, and this effect cannot be accounted for by offspring genotype [14]. It has been recognised for a long time that the causal link between parents and offspring –that forms the basis of all forms of heredity – is the transmission of some factor across generations [15]. By focusing on the nature of the transmitted factor, we can distinguish hereditary effects mediated by the transmission of genetic alleles (genetic inheritance) from effects mediated by the transmission of other factors (nongenetic inheritance, which encompasses parental effects in the broadest sense) [3]. Nongenetic parental effects can be mediated by the transmission of epigenetic, somatic, morphological, behavioural, or environmental variants [3,16,17]. Thus, a paternal effect can be said to occur when a nongenetic factor is transmitted from a male to his offspring, resulting in effects on offspring development. The nature of this nongenetic factor can be influenced by paternal genotype (paternal indirect genetic effect), paternal environment (paternal environmental effect), or a combination of both. The term 'paternal effect' has sometimes been used to refer to direct genetic effects (i.e., the transmission of alleles from males to their offspring) (e.g., [18–20]) or genomic imprinting effects (e.g., [21]), but this usage should be avoided because, in these cases, variation in offspring phenotype reflects variation in offspring genotype [14].

How then are nongenetic factors transmitted from a male to his offspring? It is easy to see how mothers can transmit biomolecules (e.g., nutrients or hormones), environmental influences (e.g., temperature or natal environment), or behaviour (e.g., maternal care or anxiety) to their offspring. Likewise, various channels of father–offspring influence are available in species that exhibit substantial paternal investment, such as ejaculate-borne defensive alkaloid compound transfer in the moth *Utetheisa ornatrix* [22], direct transfer of antimicrobial compounds to brooded eggs in the blenny *Ophioblennius atlanticus* [23], or postnatal paternal care in the mouse *Peromyscus californicus* [24]. However, paternal

Corresponding author: Bonduriansky, R. (r.bonduriansky@unsw.edu.au).
Keywords: maternal effects; paternal effects; parental effects; nongenetic inheritance; differential allocation.

0169-5347/
 http://dx.doi.org/10.1016/j.tree.2014.07.009

Box 1. Three types of paternal effect that are mediated to varying degrees by maternal responses

Type A

In species where males interact directly with their offspring, such as some vertebrates and arthropods that exhibit complex forms of paternal care, paternal effects can occur via direct effects of males on their offspring. Such effects can, for example, involve paternal behavioural influences on offspring development [24]. Nonetheless, paternal effects can interact with maternal effects in such systems (Figure I).

Type B

In external fertilisers, paternal effects can occur via male influences on eggs outside the body of the female. Such effects can be mediated by sperm- or ejaculate-borne factors [26–28], or by secretions from somatic glands [74]. There has been little contention in classifying Type B effects as paternal effects because, even though the egg phenotype can influence the effect, and different egg phenotypes can respond differently to sperm produced by different males, there is no opportunity for females to adjust egg phenotype after eggs have been released: the causal pathway is limited to responses by the egg cell itself. However, an interaction between paternal and maternal effects can still occur, and affect relative allocation to different offspring traits. For example, in an external fertiliser, eggs fertilised by males of phenotype p_1 might grow more quickly but hatch at a smaller body size, whereas eggs fertilised by males of phenotype p_2 might grow less quickly but hatch at a larger body size. Such responses might represent a facultative maternal or paternal strategy or, alternatively, a nonadaptive interaction.

Type C

In internal fertilisers, male phenotype can exert an influence on the female body, and this influence can, in turn, manifest as an effect on offspring development. Such paternal effects can encompass a complex chain of maternal responses involving the nervous, endocrine, and other physiological systems [1,5,24]. Type C paternal effects can be mediated by female differential allocation of total resources (e.g., making larger or higher-quality offspring in response to particular male phenotypes [35,36]) or, potentially, differential relative allocation to different offspring traits or fitness components (e.g., producing offspring that grow faster but are less viable in response to particular male phenotypes). Type C effects might be especially challenging to interpret because in many cases it will be difficult to determine how the effect is mediated and whether it represents a male strategy, a female strategy, or a combination of both.

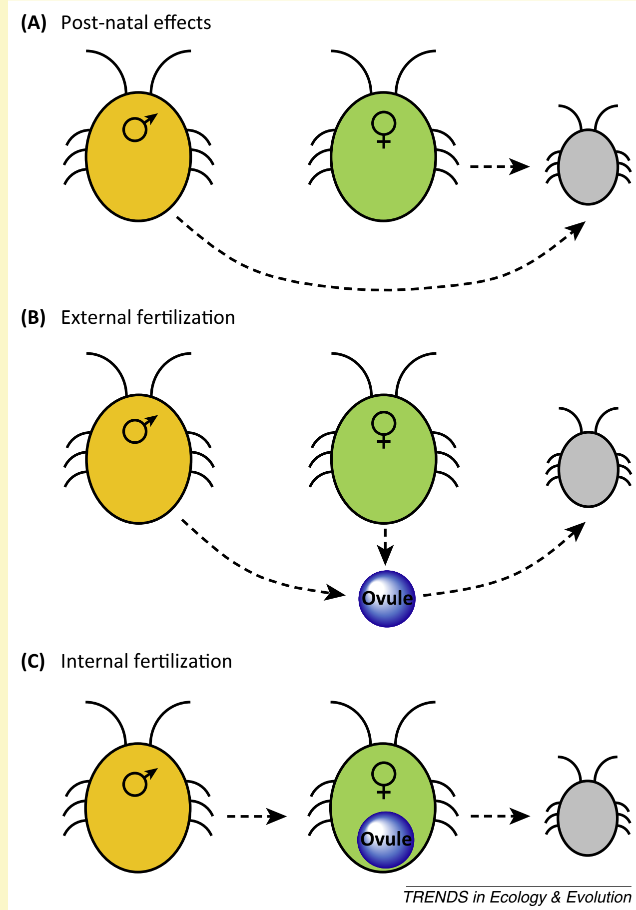

Figure I. Three basic types of paternal effect. Broken lines represent pathways whereby fathers (♂) and mothers (♀) influence their offspring. **(A)** Postnatal effects. **(B)** External fertilization. **(C)** Internal fertilization.

investment is low in most species [25], and the resulting lack of opportunity for father-offspring influence was long regarded as a constraint on the occurrence of paternal effects. Nonetheless, recent evidence shows that sperm can convey many nongenetic (e.g., cytoplasmic or epigenetic) factors [26,27], and that ejaculates contain a complex blend of proteins and lipids that can influence offspring development [28]. For example, in golden hamsters, ejaculate components produced by the male accessory glands influence offspring embryonic development, postnatal growth, and adult responses to olfactory and auditory cues [29–31]. Sperm- and ejaculate-borne factors have the potential to mediate paternal effects in all sexually reproducing species.

Importantly, however, many pathways of father–offspring influence are mediated by maternal responses. The nature of these pathways reflects a fundamental asymmetry between maternal and paternal investment, and represents a basic difference between a typical maternal effect and common types of paternal effects (Box 1). Given that eggs contribute a larger quantity of cytoplasm to the zygote than do sperm, and the egg controls early development [32], we suggest that the maternally derived composition and structure of the egg will often play a role in mediating paternal effects. Moreover, in taxa with internal fertilization, paternal effects are likely to be mediated by a complex chain of maternal physiological or behavioural responses. For example, in mice, the social upbringing of a male was found to influence the nursing behaviour of its mate, and this maternal response in turn affected the growth rate of the offspring [33]. By contrast, mothers typically exert direct effects on egg content and structure and, in many organisms, on embryonic (and sometimes postnatal) development as well. The evolutionary consequences of these fundamental differences between maternal and paternal effects have not been fully explored.

Paternal or maternal?

When paternal influences on offspring are mediated by maternal responses (Box 1), we run into an obvious conundrum: should these effects be regarded as paternal effects or maternal effects? The logic of analysis of variance (ANOVA) suggests the most straightforward decision rule. Statistically, an effect occurs when variation in an independent variable is associated with variation in the response (dependent variable). Note that, although a key assumption of such analysis is that the parent–offspring correlation is causal [14], the nature of the causal pathway