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REVIEW

Environmentally induced (co)variance in sperm and offspring phenotypes as a source of epigenetic effects

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ABSTRACT

Traditionally, it has been assumed that sperm are a vehicle for genes and nothing more. As such, the only source of variance in offspring phenotype via the paternal line has been genetic effects. More recently, however, it has been shown that the phenotype or environment of fathers can affect the phenotype of offspring, challenging traditional theory with implications for evolution, ecology and human *in vitro* fertilisation. Here, I review sources of non-genetic variation in the sperm phenotype and evidence for co-variation between sperm and offspring phenotypes. I distinguish between two environmental sources of variation in sperm phenotype: the pre-release environment and the post-release environment. Pre-release, sperm phenotypes can vary within species according to male phenotype (e.g. body size) and according to local conditions such as the threat of sperm competition. Post-release, the physicochemical conditions that sperm experience, either when freely spawned or when released into the female reproductive tract, can further filter or modify sperm phenotypes. I find evidence that both pre- and post-release sperm environments can affect offspring phenotype; fertilisation is not a new beginning – rather, the experiences of sperm with the father and upon release can drive variation in the phenotype of the offspring. Interestingly, there was some evidence for co-variation between the stress resistance of sperm and the stress resistance of offspring, though more studies are needed to determine whether such effects are widespread. Overall, it appears that environmentally induced covariation between sperm and offspring phenotypes is non-negligible and further work is needed to determine their prevalence and strength.

KEY WORDS: Epigenetics, Paternal effects, Sperm

Introduction

Classic quantitative genetics theory assumes that sperm are vehicles for genes and nothing more. Under such a view, any phenotypic covariance between sperm and the subsequent offspring they produce is due to genetic covariance between sperm phenotype and sperm genotype. In other words, any covariation between sperm and offspring phenotypes is driven by genetic effects. More recently it has been shown that for a range of taxa, environmental effects can alter the phenotype of sperm, and this environmentally induced variation in sperm phenotype can have consequences for the phenotype of offspring (Bonduriansky and Day, 2009; Bonduriansky and Head, 2007). Below, I review the environmental sources of variation in sperm phenotype and how this variation affects offspring phenotype.

Environmental sources of sperm phenotypic variation

Sperm experience two environments – the paternal environment while being produced and stored in the father, and the post-release environment: both environments can generate intraspecific variation in the phenotype of sperm that ultimately fuse with the egg. I will deal with each of these environments separately.

Paternal environment – what affects the phenotype of sperm that males release?

Within species, the sperm that males release vary in their phenotype substantially but the causes of this variation remain poorly understood. A number of reviews highlight significant variation in sperm morphology, longevity and motility both within and among males (Morrow and Gage, 2001; Pitnick et al., 2008a; Ward, 1998). Some of this variation is clearly genetically based [sperm morphology evolves under experimental evolution (Pitnick et al., 2008a)]. Nevertheless, sperm phenotype also covaries with the paternal phenotype or paternal environment, and it is this non-genetic variation that is relevant to this review. For example, non-genetic factors such as size, age and condition can vary with sperm morphology in some species but not others (Devigili et al., 2013; Johnson et al., 2013; Pitnick et al., 2008a; Rakitin et al., 1999; Schulte-Hostedde and Millar, 2004). Sperm morphology can also vary in time (Lüpold et al., 2012) and space (Laskemoen et al., 2013; Manier and Palumbi, 2008; Marks et al., 2008; Schmoll and Kleven, 2011). This variation in sperm morphology contrasts with classic theory that predicts a single optimal sperm phenotype that should maximise male fertilisation (Parker, 1993; Pitnick et al., 2008a). Indeed, experimental evolution studies show that consistent selection under sperm competition reduces variation in sperm phenotype (reviewed in Pitnick et al., 2008a). More recently, however, there has been growing evidence that selection on sperm phenotype is context dependent, such that different phenotypes will be favoured under different conditions (Crean and Marshall, 2008; Fitzpatrick et al., 2007). For example, Johnson et al. (Johnson et al., 2013) showed that when sperm were able to access eggs immediately, sperm with long tails and smaller heads were favoured, but when sperm accessed eggs after ageing, sperm with larger heads were favoured. Differential selection on sperm phenotypes under different conditions has, in some species at least, led to the evolution of gamete plasticity whereby males adaptively adjust the phenotype of their sperm in accordance with their local environment.

One of the strongest selection pressures that males face is sperm competition from other males. Accordingly, a number of studies have shown that males adjust the phenotype of their sperm in response to their perceived risk of sperm competition. For example, males alter the phenotype of their sperm according to mating mode, social status and the density of other males in groups as diverse as fish, chickens, ascidians, annelids and humans (Crean and Marshall, 2008; Fitzpatrick et al., 2007; Immler et al., 2010; Johnson et al., 2013). Crean and Marshall (Crean and Marshall, 2008) showed that males alter the phenotype of their gametes in response to increases in the risk of sperm competition, and that this gamete plasticity resulted in higher fertilisation success when sperm concentrations were high. Gamete plasticity in response to sperm competition is not

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universal, however: Janicke and Schärer (Janicke and Schärer, 2010) found no evidence for changes in sperm morphology in response to sperm competition in flatworms, despite major changes in sex allocation between treatments. Nevertheless, gamete plasticity in response to sperm competition represents an important source of variation in sperm phenotype in a range of species and therefore a potential source of non-genetic effects. While sperm competition is a strong selection pressure that generates gamete plasticity, and therefore an important driver of variation in sperm phenotypes, it is not the only selection pressure to which males respond.

Environmental stress can generate variation in sperm phenotypes and, in some cases, this variation appears to be driven by adaptive gamete plasticity. For example, when males of the marine tubeworm *Hydroides diramphus* are exposed to hyposaline seawater, they alter the morphology of their sperm and these sperm are better able to cope with hyposalinity themselves (Jensen et al., 2014). This effect was unequivocally non-genetic because fathers were able to alternate between producing hyposalinity-tolerant sperm and normal sperm depending on the environment they most recently experienced. Other studies show similar changes in the stress resistance of sperm following parental exposure to that stress, suggesting that gamete plasticity in response to stress may be more widespread among external fertilisers than is currently appreciated (Hintz and Lawrence, 1994; Parker et al., 2012; Roller and Stickle, 1994; Tait et al., 1984; but see Adriaenssens et al., 2012). Given the particular sensitivity of sperm to environmental stressors (Marshall, 2006), I predict that gamete plasticity in response to local environmental conditions is most common in external fertilisers that release their sperm directly into the environment (e.g. most marine invertebrates, most fish and amphibians) and less common in internal fertilisers, but this remains to be tested.

Overall then, it seems that many factors can generate substantial variation in the phenotype of sperm before release from their fathers (Fig. 1). Table 1 summarises the environmental sources of variation in sperm phenotypes that are driven by the paternal environment or phenotype.

Post-release environment

The environment into which the sperm are released (the post-release environment) may alter the phenotype of sperm that access eggs in two ways: (i) through the phenotypic alteration of the sperm; and (ii) by the phenotype-dependent performance of sperm in the post-release environment. Sperm, upon release from the fathers, are immediately exposed to a range of factors, which can alter the phenotype of the sperm that will go on to fuse with eggs. While the physical traits of the sperm may be unaltered by environmental conditions, it is unclear whether other, more labile traits are unaffected by the conditions that sperm experience. In other words, it is unclear whether sperm exhibit phenotype plasticity themselves. Several studies show that sperm alter their behaviour in response to different environmental conditions (Bolton and Havenhand, 1996), and so it is reasonable to expect that other non-behavioural traits may similarly change with the environment. Thus, even if sperm are identical in their phenotypes upon release, the post-release environment has the, largely unexplored, potential (but see Ritchie and Marshall, 2013) to alter the phenotype of sperm and generate phenotypic variation where there was otherwise none.

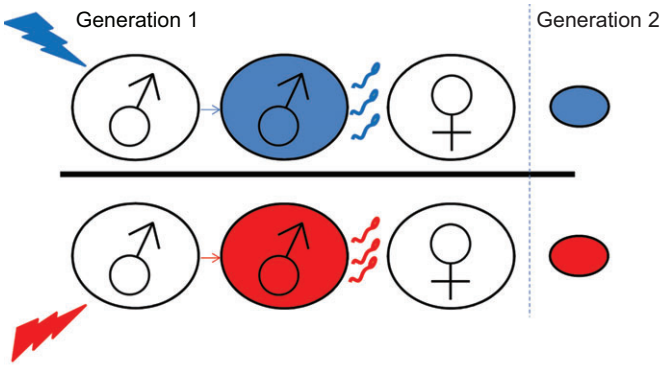

Fig. 1. Schematic diagram describing how the pre-release environment can generate phenotypic co-variation between sperm and offspring phenotypes. Different environmental effects (indicated by different coloured lightning bolts) affect fathers with similar genotypes such that each father alters their phenotype and the phenotype of their sperm via gamete plasticity (as indicated by the different colours). The different phenotypes of sperm then generate offspring with different phenotypes in the subsequent generation via either maternal effects or direct phenotypic effects of the sperm on offspring phenotype.

The post-release conditions can also exert significant selection on existing phenotypic variation. If the environment favours one sperm phenotype over another, then that phenotype will be differentially successful, effectively changing the mean phenotype of sperm that fuse with eggs relative to the mean phenotype of sperm that were released from the male. For example, Fitzpatrick et al. (Fitzpatrick et al., 2012) found that slower swimming sperm were more likely to fertilise eggs than faster swimming sperm in the mussel *Mytilus galloprovincialis*. Environmental stressors in external fertilisers in particular are likely to bias which sperm phenotypes successfully fertilise eggs. Even within an ejaculate from a single male, sperm phenotypes often vary significantly such that environmental factors could bias which sperm phenotypes go on to successfully fertilise eggs (Fitzpatrick et al., 2010; Pitnick et al., 2008a). For example, Ritchie and Marshall (Ritchie and Marshall, 2013) found that the post-release salinity environment that sperm experience strongly affects which sperm access eggs. When sperm of the estuarine tubeworm *Galeolaria geminoa* are exposed to low salinity, only a subset of sperm are tolerant to low salinity and only this subset go on to fertilise eggs (Ritchie and Marshall, 2013). Similarly, Crean et al. (Crean et al., 2012) found that when sperm cannot access eggs immediately, only a subset of sperm are sufficiently long lived to go on to fertilise eggs. In each of these examples, a non-random subset of sperm phenotypes (hyposaline tolerant and longer lived) access the eggs; the rest are 'filtered out' by the post-release environment (Fig. 2). Likewise, in an almost identical experiment on Atlantic salmon, the timing of access to eggs affected the subsequent phenotype of offspring (Immler et al., 2014). Numerous environmental factors induce mortality in the sperm of external fertilisers, including temperature, pH and toxicants (Marshall, 2006) – if this mortality is non-random with respect to sperm phenotype, then all these environmental factors could generate variation in the phenotype of sperm that access eggs. Interestingly, White et al. (White et al., 2014) found that the pH environment (low versus ambient) in which fertilisation took place affected subsequent offspring performance regardless of whether offspring experienced a low pH or not. While this effect of lowered pH may have affected eggs directly, the alternative is that pH differentially affected some sperm over others such that only low pH-tolerant sperm fertilised eggs.

Environmental filtering and selection for different sperm phenotypes is not restricted to external fertilisers. In species with internal fertilisation, paternity can be biased towards those sperm that swim the fastest, have the greatest motility or suffer the least mortality in the reproductive tract (Evans et al., 2003; Pizzari et al.,

Table 1. Summary of published effects of male phenotype or environment on sperm phenotype

Study	Species	Environment	Response
Vermeulen et al., 2009	*Panorpa vulgaris* (scorpionfly)	Density	Group-bred males had smaller sperm
Morrow et al., 2008	*Drosophila melanogaster* (fruit fly)	Density × body size	Larger males produced larger sperm in some environments
Rahman et al., 2013	*Poecilia reticulata* (guppy)	Diet quality (carotenoid content)	Decrease in sperm size with poor nutrition
Lüpold et al., 2012	*Agelaius phoeniceus* (blackbird)	Harem size	Increase in flagellum:head ratio
Green, 2003	*Aleochara bilineata* (rove beetle)	Male age	Older males produced larger sperm
Gasparini et al., 2010	*Poecilia reticulata* (guppy)	Male age	Older males produced longer sperm
Iwata et al., 2011	*Loligo bleekeri* (squid)	Male mating type	Sneaker males produced larger sperm
Devigili et al., 2013	*Poecilia reticulata* (guppy)	Male nutrition	No effect
Hellriegel and Blanckenhorn, 2002	*Scathophaga stercoraria* (dung fly)	Male nutrition	No effect
Green, 2003	*Aleochara bilineata* (rove beetle)	Male nutrition	No effect
Vermeulen et al., 2009	*Panorpa vulgaris* (scorpionfly)	Male nutrition	Food-restricted males produced larger sperm
Skinner and Watt, 2007	*Poecilia reticulata* (guppy)	Male size	Larger males produced larger sperm
Schulte-Hostedde and Montgomerie, 2006	*Nerodia sipedon* (water snake)	Male size	No effect
Durocher-Granger et al., 2011	*Trichogramma euproctidis* (egg parasitoid)	Male size	Larger males produced larger sperm
Locatello et al., 2008	*Gambusia holbrooki* (mosquito fish)	Male size	No effect
Helfenstein et al., 2008	*Riparia riparia* (sand martin)	Male size	No effect
Gage et al., 1998	*Salmo salar* (Atlantic salmon)	Male size	No effect
Green, 2003	*Aleochara bilineata* (rove beetle)	Male size	Larger males produced larger sperm (younger males only)
Johnson et al., 2013	*Galeolaria gemineoa* (tubeworm)	Male size	Larger males produced sperm with smaller heads
Amitin and Pitnick, 2007	*Drosophila melanogaster* (fruit fly)	Male size	Larger males produced larger sperm
Vladić et al., 2002	*Salmo salar* (Atlantic salmon)	Male size	No effect
Dowling et al., 2007; Gay et al., 2009	*Callosobruchus maculatus* (seed beetle)	Maternal age	Older mothers produced sons that produced longer sperm
Jensen et al., 2014	*Hydroides diramphus* (tubeworm)	Salinity	Males in hyposalinity produced sperm with smaller heads
Cramer et al., 2013	*Troglodytes aedon* (wren)	Season	Increase in flagellum:head ratio
Lüpold et al., 2012	*Agelaius phoeniceus* (blackbird)	Season	Increase in flagellum:head ratio
Immler et al., 2010	*Erythrura gouldiae* (Gouldian finch)	Sperm competition	Change in morphology
Crean and Marshall, 2008	*Styela plicata* (sea squirt)	Sperm competition/ density	Increase in sperm size
Janicke and Scharer, 2010	*Macrostomum lignano* (flatworm)	Sperm competition/ density	No effect
Minoretti et al., 2013	*Arianta arbustorum* (snail)	Temperature	Decrease in sperm size with temperature
Blanckenhorn and Hellriegel, 2002	*Scathophaga stercoraria* (dung fly)	Temperature	Decrease in sperm size with temperature
Adriaenssens et al., 2012	*Gambusia holbrooki* (mosquito fish)	Temperature	Increase in sperm size with temperature

2008). This bias in fertilisation according to sperm phenotype can arise from sperm outcompeting each other, or cryptic female choice whereby females differentially fertilise their eggs with different sperm (Birkhead, 1998; Pizzari and Parker, 2008). For example, sperm mortality in the female reproductive tract can be exceedingly high and specific to the identity of the mating male, raising the potential at least for non-random selection of sperm phenotypes (Bernasconi et al., 2002). Finally, the phenotype of the sperm can be

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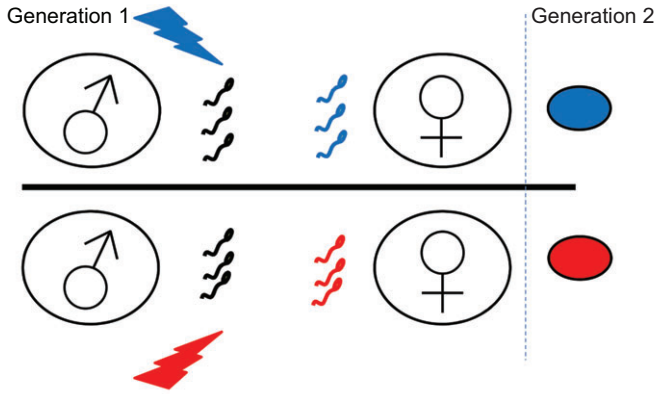

Fig. 2. Schematic diagram describing how the post-release environment can generate phenotypic co-variation between sperm and offspring phenotypes. Different environmental effects (indicated by different coloured lightning bolts) affect the phenotype of sperm from fathers with similar genotypes. These environmental effects then induce a phenotypic change in the sperm (as indicated by the different colours) and this generates phenotypic variance in the subsequent generation.

affected as they travel through the female reproductive tract (Pitnick et al., 2008b). Regardless of the mechanism, in each instance, the mean phenotype of sperm that ultimately fertilise eggs may not be the same as the mean phenotype of sperm that were released by the males.

Overall then, phenotypic variation in sperm that actually fuse with eggs may be generated by environmental factors both before and after the release of sperm from their fathers. Adaptive and non-adaptive plasticity in sperm will generate phenotypic variation before sperm are released, and environmental filtering effects in both external and internal fertilisers will further alter the phenotype of sperm that access eggs. In the following section, I explore the consequences of such phenotypic variation.

Is fertilisation a new beginning? Phenotypic links between sperm and offspring phenotypes

Environmentally induced variation in the phenotype of sperm only has the potential to act as a source of epigenetic effects if the phenotype of sperm affects the phenotype of the offspring they sire. While traditional quantitative genetics theory assumes no link between sperm phenotype and offspring phenotype, increasingly, such links are being detected. A comprehensive review of non-genetic inheritance is beyond the scope of this review (see Bonduriansky and Day, 2009), but those non-genetic effects that are explicitly linked to sperm phenotypes will be considered here. Furthermore, several studies show that paternal environment can induce epigenetic changes in sperm that can be stably transmitted to offspring (reviewed in Jablonka and Raz, 2009), but these studies did not specifically explore whether sperm phenotypes differed, and as such are outside the scope of this review.

Effects of gamete plasticity on offspring phenotype

Paternal modifications of the sperm phenotype have been shown to have consequences for offspring phenotype. In a follow-up study to their earlier work (Crean and Marshall, 2008), Crean and colleagues (Crean et al., 2013) explored the consequences of gamete plasticity for offspring. They (Crean et al., 2013) took advantage of the life histories of external fertilisers, dividing sperm and eggs from single individuals before conducting *in vitro* fertilisations, thereby excluding potentially confounding maternal effects. They (Crean et al., 2013) showed that offspring sired by sperm from males that experienced high population densities performed better in high population densities themselves, whereas offspring sired by sperm from low population density males performed better in low population densities. The increased performance of offspring when their environment matches that of their fathers suggests that fathers may adjust the phenotype of their sperm not only for the fertilisation environment but also for the post-fertilisation environment. Such paternal effects are analogous to so-called 'anticipatory maternal effects', whereby mothers use cues from their own environment to modify the phenotype of their offspring and increase their fitness in that environment (Marshall and Uller, 2007). In biomedical studies of humans, there has been increasing speculation regarding the existence of adaptive paternal effects [e.g. the 'thrifty telomere hypothesis' (Eisenberg, 2011)], whereby males adjust the phenotype of their sperm in response to their own environment in order to increase offspring fitness. However, these hypotheses have received less attention beyond studies of humans. Whether the results found by Crean et al. (Crean et al., 2013) represent a true adaptive paternal effect or whether it was simply coincidental that offspring performance was higher when their environment matched that of their fathers remains unclear at this stage, but the results are certainly intriguing. Given the apparent prevalence of paternal modifications of sperm phenotype in response to sperm competition across a range of taxa, the consequences of these modifications should be explored further.

As discussed above, there is some evidence that males manipulate the phenotype of their sperm in response to environmental stress and this plasticity also appears to have consequences for offspring phenotypes. Jensen et al. (Jensen et al., 2014) found that exposing fathers to low salinity environments not only resulted in sperm that could cope with lower salinity but also their offspring were more tolerant of low salinity environments. This effect persisted across the larval phase and suggests the potential at least for fathers to increase the performance of their offspring when environmental conditions change, but many more tests are needed.

There are tantalising indications that sperm phenotype affects offspring phenotype in species with internal fertilisation. A number of studies have documented covariance between the phenotype of sperm and the phenotype of offspring in species with internal fertilisation. For example, more competitive sperm can produce more viable offspring (Fisher et al., 2006; Hosken et al., 2003) and more competitive sperm may produce offspring with more competitive sperm themselves [the so-called 'sexually selected sperm hypothesis' (reviewed in Pitnick et al., 2008b)]. While some of this covariance between sperm and offspring phenotypes is undoubtedly driven by genetic effects, that sperm competitive ability can be dependent on the phenotype of males [e.g. condition (McNamara et al., 2014)], raises the potential for sperm–offspring phenotypic covariance to be partly non-genetic. It is difficult, however, to unequivocally ascribe phenotypic covariance between sperm, fathers and offspring to paternally driven epigenetic effects in internal fertilisers. Numerous studies have demonstrated that mothers alter the phenotype of their offspring in response differences in male quality or sperm phenotype (Cunningham and Russell, 2000; Uller et al., 2005) and as such maternal differential allocation could therefore drive some of these patterns in internal fertilisers.

Effects of the post-release modification of sperm phenotypes on offspring phenotype

While evidence is limited, there are several studies that show that when the environment filters out specific sperm phenotypes, this has

consequences for the phenotype of offspring and is therefore an important source of epigenetic effects. Crean et al. (Crean et al., 2012) found that sperm that accessed eggs immediately after release sired offspring that differed from those sired by sperm from the same ejaculate that were prevented from accessing eggs for 1 h post-release (Crean et al., 2012). Similarly, Ritchie and Marshall (Ritchie and Marshall, 2013) found that offspring sired by sperm that had been exposed to lower salinity performed differently to offspring that were sired by sperm from the same ejaculate but that had not been exposed to decreased salinity. Such differences are remarkable given that these offspring differ substantially in their performance but remain full siblings – this finding illustrates the unanticipated strength of the effects of environmental filtering of sperm phenotypes (Ritchie and Marshall, 2013). Interestingly, the offspring sired by sperm that were exposed to low salinity were more resistant to lower salinity themselves – in other words, there is phenotypic covariance between sperm salinity tolerance and offspring salinity tolerance. The idea that traits expressed in sperm are related to offspring traits has received very little attention, but has some interesting implications I explore below.

Implications of covariance between sperm and offspring phenotypes

Ecological implications

I suggest that environmentally induced covariance between sperm and offspring phenotypes has a number of ecological implications, particularly for species with external fertilisation. At the very least, environmentally induced phenotypic covariance between sperm and offspring represents an important, yet largely unexplored, source of variation in offspring phenotypes. Once, maternal effects were considered nuisance sources of variation in quantitative genetics studies (Mousseau and Fox, 1998), whereas now their ecological role as both a conduit and a buffer of environmental variation across generations is well recognised (Benton et al., 2008). I suspect that environmentally induced sperm–offspring covariance has much weaker effects than do maternal effects, but recent studies suggest that epigenetic modifications could in fact be inherited from sperm more than eggs in some systems (Jiang et al., 2013), and as such their role should be explored. The fact that the environment that sperm experience affects offspring performance also has interesting implications for *in vitro* fertilisation in humans and associations with disease (DeBaun et al., 2003).

It is well known that environmental toxicants reduce fertilisation success in external fertilisers and may limit the quantity of offspring that are produced by a population (Byrne, 2012; Hollows et al., 2007). If environmental filtering of sperm phenotypes is common, then toxicants could also affect the quality of offspring that are produced by a population – a subtle but potentially more pervasive impact of pollution. Alternatively, if covariance between sperm and offspring tolerance to stress is more widespread, then the impacts of pollutants could be mitigated by this covariance – any offspring produced in the presence of the stress may intrinsically have higher tolerance to the stress as only stress-resistant sperm were successful in siring offspring. Either way, further tests are needed to determine the role of environmental filtering of sperm phenotypes by toxicants in the population dynamics of broadcast spawners.

Evolutionary implications

Bonduriansky and Day (Bonduriansky and Day, 2009) provide a comprehensive account of the general evolutionary implications of non-genetic inheritance, so here I will focus on those that are specific to sperm–offspring phenotypic covariance. The most interesting implication concerns gamete plasticity in males. That sperm and offspring appear to share phenotypic links suggests that fathers may be more constrained in the degree to which they can alter their sperm to maximise fertilisation success than previously realised. Under the classic view that sperm are merely transporters of genetic material to eggs, and that their phenotype only matters for ensuring fertilisation success, males should be relatively unconstrained in the way they alter their gametes – as long as a phenotypic change favours fertilisation, males should alter their gametes according to the local environment and this will have no consequences for offspring phenotype or performance. Accordingly, many studies show such gamete plasticity to maximise fertilisation success. If, however, sperm and offspring phenotypes are somewhat linked, as has been demonstrated for some species reviewed here, then paternal manipulations of sperm phenotype may not only affect fertilisation success but also alter offspring performance. Schluter et al. (Schluter et al., 1991) highlight the limits that linked life-history stages place on evolution more generally, DeWitt et al. (DeWitt et al., 1998) discuss this limit on within-generation plasticity and Marshall and Morgan (Marshall and Morgan, 2011) consider the consequences of phenotypic links for life-history evolution, so I will discuss only the most relevant issues here. Essentially, if sperm phenotype affects offspring phenotype then paternal changes to sperm phenotype may increase fertilisation success but decrease offspring performance, thereby negating any benefit of paternal gamete plasticity. This constraint may explain why gamete plasticity is not universal (Janicke and Scharer, 2010): in some instances the post-fertilisation costs of manipulating sperm phenotype outweigh the pre-fertilisation benefits. Manipulating sperm phenotype in response to environmental stress may be subject to similar constraints to those for sperm competition – I envisage that only highly predictable and strongly negative stressors are likely to evoke gamete plasticity in fathers, otherwise the downstream risks of expressing gamete plasticity (relative to the benefits) may be too great. Formally considering environmental predictability from the perspective of fathers (Burgess and Marshall, 2014) may result in more targeted studies of sperm plasticity.

Future directions

Throughout all of my discussions of environmentally induced sperm–offspring phenotypic covariance, one obvious element has been absent – mechanism. As far as I'm aware, we have very little understanding of the mechanistic basis of how sperm phenotype affects offspring phenotype. There is evidence that RNA in sperm can affect sperm phenotype and this may be the source of the effect (Cuzin et al., 2008; Youngson and Whitelaw, 2008). Alternatively, sperm phenotype may covary with other components of the ejaculate, and the ejaculate rather than the sperm may drive phenotypic changes in the offspring (Bonduriansky and Day, 2009). Disentangling the effects of the ejaculate and the sperm would be more straightforward in species with external fertilisation rather than internal fertilisation. Methylation would seem another fruitful path to explore – it should be possible to examine how the methylome of offspring varies with the phenotype of the sperm that sired them (Jiang et al., 2013; Molaro et al., 2011).

The mechanism underlying the effects of environmental filtering on sperm remains unknown. I have assumed that such effects are the result of phenotype-specific removal of sperm, in essence selection on one sperm phenotype over another. For some phenotypes and environments (sperm competitive ability), this mechanism seems likely, but for others (e.g. longevity, toxicants), this mechanism is less

likely. Rather than a selection effect, environmental-filtering effects on sperm phenotype may simply be the result of damage to the DNA of sperm – such effects could be examined using a number of standard assays (Agarwal and Allamaneni, 2005; Tice et al., 2000).

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