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Abstract: The article discusses the development of competition among sexes for sexual reproduction. It points out that males and females fight to get the maximum reproductive output for the minimum input. Recalled are the views related to the competition for sexual reproduction, including the male-centered perspective of English physician William Harvey and another by Antonie Leeuwenhoek who was dubbed the father of the microscope. The explanation of Charles Darwin on sexual selection and the importance of female mate choice is also included.

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Dad V Mom: the ultimate battle of the sexes

Producing babies is not the happy, collaborative affair you might think. Even before conception, males and females fight it out to gain control over their offspring

EVEN the most romantic evolutionary biologist knows that sexual reproduction is rarely a harmonious affair. Among most higher animals it is often predicated on fierce fighting, showy

one-upmanship, exploitation and deception. Charles Darwin himself drew the battle lines, when he set out his ideas on sexual selection to explain the evolution of traits that provide mating advantages - either through contests between members of the same sex or by increasing attractiveness to the opposite sex. Much of what Darwin said still guides our thinking. However, since the mid-19th century it has become clear that there is more to successful reproduction than mere copulation.

Producing offspring is both expensive and something of a gamble: ideally you want a partner with good-quality genes that are compatible with your own, and someone to provide effective and reliable childcare. Getting your offspring safely from conception to adulthood is a huge investment, so the question of which partner has control over the process is very important. We now know that the competition to get genes into the next generation is fought on many fronts, often on unseen ground within the female reproductive tract, and that victory does not always lie where it might appear.

In evolutionary terms, and sometimes in real terms, males and females fight to get the maximum reproductive output for the minimum input. Identifying which sex wins has a long history and remains a highly controversial area of biology that is still full of surprises. Yet the question of who prevails in this particular battle of the sexes is too tempting to dismiss. So, drawing on the most recent discoveries and our own experience on the frontline of this research, we consider how attitudes have see-sawed over the centuries and attempt to identify which sex really has the upper hand when it comes to reproduction.

From the early days of civilisation, people noted the presence of eggs in the natural world and recognised their great importance. Eggs seemed to be where life began, and this observation had a profound influence on many aspects of ancient societies and religions. The idea of a cosmic egg, from which all living things arose, was widespread as a creation myth. Nature was logically viewed as a female figure and the egg a powerful symbol of fertility. Even now, we still refer to "mother nature" and the egg remains central to our Easter celebrations.

Early civilisations knew that eggs were produced by females, but they had almost no idea about the male contribution to reproduction. Even by Homer's day in the 9th and 8th centuries BC, females were thought to become pregnant through "something in the air" or possibly by a divine stimulus. Some 400 years later, Pythagoras and then Aristotle promoted the idea that it was not the air, nor God, but the male who contributed that all-important "something", and the female was relegated to a mere vessel in which the embryo developed. So was born a homocentric view of reproduction that changed little for several hundred years. Even the 17th-century anatomist Hieronymus Fabricius, aka "the father of embryology", believed that "semen perfects the egg".

This male-centred view was eventually challenged in 1651 by the celebrated English

physician William Harvey in his *Disputations Touching the Generation of Animals*. Harvey, like many others, believed that semen transfer was involved in reproduction but he wanted to find out exactly how. That's where his troubles began. In his numerous dissections, he tried and failed to find evidence of a role for semen within the female body. So he reluctantly came to the conclusion that "all that is alive comes from the egg".

It wasn't long, however, before the homocentric view got a renewed boost. In 1677, a Dutch draper called Antonie Leeuwenhoek, dubbed the "father of the microscope", discovered that the semen of humans and other animals contained thousands of "animalcules". He correctly identified these as that special something needed for the creation of a new individual. Despite the great disparity in size between eggs and sperm, the idea that the male contribution was uppermost sat well with the male-dominated scientific community. There was much talk of "preformation": the idea that inside each sperm a tiny preformed human was biding its time until an egg should provide it with a suitable place to grow. Nicolaas Hartsoeker, an obliging pupil of Leeuwenhoek's, even produced what became an iconic drawing of the homunculus he thought he could see curled up inside a human sperm.

Still, not everyone was taken in. The sceptics included John Ray, another key 17th-century figure, the father of natural history. In his 1691 book *The Wisdom of God*, Ray recognised that preformation was unlikely since many of the poor homunculi would be doomed if only one sperm was needed for each egg, as Leeuwenhoek thought. In an early version of the Monty Python credo "every sperm is sacred", Ray contended that "God cannot be that wasteful". Other detractors of the idea also wondered how far preformation could be taken, envisaging ever smaller homunculi nestling inside the testicles of each homunculus like a series of Russian dolls.

Equal opportunities?

With some biologists still arguing for the primacy of the egg, scientific opinion became polarised - ovists and spermists wrangled over who had the upper hand in reproduction well into the 19th century. However, with the discovery of fertilisation by the German biologist Oscar Hertwig in 1857, the observed union of egg and sperm gave rise to the idea that offspring were in fact a blend of their two parents. There was a problem, though. While some features of offspring did indeed seem to fit this pattern, many did not. Even Darwin dabbled with the blending theory before coming to the conclusion that this was not the major principle of inheritance and that science did not yet have the answer.

Enter Gregor Mendel. His experiments in the mid-19th century on the inheritance of simple traits in peas - apparently unknown to Darwin although he and Mendel were contemporaries - provided the answer. After random mixing of genes to create eggs and sperm, offspring inherit one functionally equivalent form of each gene from each parent. Since some of these

"alleles" are dominant over others, simple blending does not apply. Sometimes an allele from the mother would win out and sometimes one from the father.

If the dawn of genetics generated a somewhat uneasy truce between ovists and spermists, Darwin's ideas about sexual selection stoked the flames of competition again. In his controversial 1871 book *The Descent of Man, and Selection in Relation to Sex*, Darwin argued that individuals of both sexes evolve the morphology and behaviour most likely to provide them with highest success in the mating game.

Darwin's focus on traits that influence the success of males in competition for access to females encouraged many contemporaries to view females as largely a prize rather than a participant in mating. As the British biologist Walter Heape stated in 1913, the male "hunts for his partner and is an expender of energy: the female is passive, sedentary, one who waits for her partner". However, Darwin also argued that female choice could drive the evolution of secondary sexual characteristics in males. But the idea that females might pick and choose males for their own ends didn't wash with the Victorian establishment. Women, let alone females of other species, surely did not have the cognitive capacity to be so discerning.

Research by behavioural and evolutionary ecologists now tells us that Darwin was right about the importance of female mate choice. Far from being passive players, female choice is an important driver of sexual selection. What's more, discriminating females direct the course of reproduction far beyond the mating process itself and in ways that Darwin could hardly have imagined.

We are all familiar with the elaborate ornaments and weaponry developed mainly by males to win pre-copulatory contests - think of the peacock's tail or the stag's antlers. Much less well known are the complex internal structures and tricks that females have evolved to increase their control over which sperm actually fertilise their eggs. In many species, females mate with more than one male and after sperm enter the female reproductive tract, so-called cryptic female choice can take place through a range of mechanisms, including selective sperm storage and sperm ejection.

Males have of course risen to this challenge. In an escalation of the reproductive power struggle, they have evolved all manner of countermeasures to foil female interference. These include strategies and structures to enhance their prospects of winning the competition with other males' sperm and avoid expulsion from the female reproductive tract. Very recently, for example, researchers at Harvard University discovered that when sperm from several male deer mice are present in the female reproductive tract, the sperm from the same male can recognise and hook up with one another. Joining forces as a brotherhood in the race to get to the egg allows them to travel faster, increasing the chances that one of their number will hit the jackpot (*Nature*, DOI: 10.1038/news.2010.22).

You might think that once fertilisation has occurred the game is over - after all each sex makes an equal genetic contribution to their offspring. You would be wrong. Just getting your genes into offspring is not enough. New evidence is emerging that the arms race continues even after fertilisation, with the two sexes battling it out over whose genes will be most influential in shaping the biology and behaviour of their offspring and how much time and energy must be invested in them.

One important card that females have to play is the sheer size of the egg relative to the sperm. In addition to the genes and some crucial nutrients, eggs also contain a cocktail of hormones, organelles, antibodies, antioxidants and RNAs, all of maternal origin. These are known to influence growth, hormonal balance, personality, behaviour, and possibly even sex in some cases. In the past 15 years, there has been a substantial increase in investigations into the nature of these maternal effects on offspring, and also whether they can be manipulated by females according to circumstances. We now know, for example, that female birds alter the levels of testosterone in the yolk of their eggs depending on the anticipated hatching order of the chicks, social conditions where they are nesting, and even the attractiveness of the father. Increasing testosterone can make some nestlings more competitive than others.

Express yourself!

That's not all. Recent research shows that contrary to what was previously supposed sperm also contribute more than just genes to the egg. In many mammals it is not just the DNA-containing sperm head that penetrates the egg - the whole thing, tail and all, goes in, transferring thousands of messenger RNAs and proteins. These might be involved in directing embryo development, perhaps even counteracting some instructions from the egg cytoplasm. Some of these male RNAs are of the type that controls gene expression, so their effects on the embryo could be very important, since gene activity must be finely orchestrated in the development of an embryo. As yet, their role is unclear.

Nonetheless, the latest line of research suggests the egg still has the upper hand. This comes from a burgeoning interest in so-called "epigenetic effects" - changes in the way genes are expressed without the need to alter the DNA sequence itself.

Inside a cell, genetic material takes the form of a complex package of DNA and histone proteins called chromatin. It is modification of this structure - commonly by adding a methyl group in a process known as methylation - that leads to epigenetic effects. Epigenetic effects can be induced by signals from within the cell or from other cells. Exposure to nutritional, chemical or physical environmental factors such as food shortage or temperature changes can result in lifelong changes for the organism. Sometimes epigenetic effects are even passed on to the next generation, in which case the process is known as genomic imprinting. It

is this that provides another arena for sexual conflict - if one parent selectively switches off or "silences" genes coming from the other. Here females seem to win out.

With genomic imprinting, which gene is expressed depends on which parent it came from. Of course, this contravenes one of the basic tenets of Mendelian genetics - that alleles from the mother and father are functionally equivalent. Nevertheless, genomic imprinting has so far been identified in a small number of organisms - mostly mammals and flowering plants, with possibly a few fishes. While only a few genes have been implicated they appear to be significant. The imprinted genes include several with a role in embryo growth and development, most of which are also expressed in the brain, meaning that key traits like body size, cognitive ability and personality might be moulded by epigenetic inheritance.

One intriguing observation is that genomic imprinting appears to be associated with species in which the mother nurtures the embryo inside her body, so contributing far more to its survival than does the father. This leaves mothers potentially open to exploitation if fathers could manipulate gene expression in their offspring so as to further increase maternal investment in the embryo. But once again, females are a step ahead.

Genomic imprinting is rare because most of the methyl groups that have accumulated on DNA over an individual's lifetime are stripped away following fertilisation. However, some do make it through to the next generation - and a few years ago a team led by Toru Nakano at Osaka University in Japan, discovered that mothers appear to manipulate this process. They found that demethylation mostly affects the DNA that embryos inherit from the father, while the mother's DNA is protected by a special protein in the egg produced by a gene called stella (Nature Cell Biology, vol 9, p 64). So, at the last post, where there is a conflict over control of offspring development and the level of investment in its growth, victory seems to lie firmly with the mother. It looks like eggs rule after all.

This maternal control of growth and development has some fascinating implications. It means that, for many of the traits important in the mating game, such as body size and brain function, the father's genes might not be as influential as the mother's. So perhaps the fine details of what a particular male looks like are not as important to females as biologists have been apt to think. Instead, what females could really be after when they choose the sperm of one male over another is the male whose genes they can most easily manipulate behind the scenes. If so, that calls for a huge shake-up in the way we view sexual selection.

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