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## How stupid not to have thought of that: post-copulatory sexual selection

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### Abstract

Science progresses through ideas or hypotheses; novel ways of viewing the world. If those ideas survive testing, then they are considered ‘the truth’, or more crucially, truth-for-now, for the essence of science is that if a new idea provides a better explanation of the way the world is, the truth changes. Darwin’s idea of evolution by natural selection, published as the *Origin* in 1859, replaced the earlier truth of physico- or natural-theology introduced by John Ray in 1691. Despite resistance by the church, Darwin’s truth gained widespread acceptance, in part due to the efforts of T. H. Huxley, who on reading the *Origin* said ‘How extremely stupid not to have thought of that!’ Despite natural selection’s enormous explanatory power, there were certain phenomena it apparently could not explain, including female promiscuity. It was only in the 1960s when natural selection was viewed as operating explicitly on individuals (rather than populations or groups), that this changed. Rather than being a cooperative venture between the sexes, sexual reproduction was now viewed in terms of conflicts of interests, and in so doing provided an explanation for female promiscuity (albeit in a male-biased sort of way). Until this point, sexual selection had been concerned exclusively with mate acquisition. With an evolutionary perspective focussing on individuals, it was recognized that sexual selection might continue after insemination, and that rather than competing for partners, males compete for fertilizations. Later it was acknowledged that females, through cryptic processes can also influence the outcome of sperm competition. Today, post-copulatory sexual selection provides explanations for many previously bewildering reproductive traits, including the extraordinary diversity in male and female genitalia, the design of spermatozoa and ova, of seminal fluid and of copulation behaviour itself

### Introduction

Thomas Henry Huxley played a vital role in promoting Darwin’s concept of evolution by natural selection. Most famously, on 30 June 1860, at a meeting of the British Association for the Advancement of Science – a meeting some later described as the most memorable of their lives – Huxley ran circles round Soapy Sam, the Bishop of Oxford, over who had the right – theologians or scientists – to explain the origin of species. Darwin wasn’t there – luckily – for as he knew full well, had he been, his gentle manner may have meant losing to the bishop. Instead, bulldog Huxley, together with Darwin’s closest friend, Joseph Hooker, ably defended the scientific viewpoint. On the Bishop’s side was the Bible-touting Captain Fitzroy, with whom Darwin had shared a dinner table on the *Beagle*, and with whom Darwin had crossed swords over science and religion on more than one occasion during their long voyage (Desmond, 1994, 1997). Others in the Oxford audience,

including the ornithologist Henry Tristram (later Canon Tristram), were unconvinced by the scientific case. Tristram had been persuaded by Alfred Newton – Britain’s leading ornithologist – to interpret some of his ornithological results in terms of natural selection. However, the Oxford meeting changed Tristram’s mind about Darwin and he told Newton, who was sitting next to him, that from now on he was an anti-Darwinian. Tristram objected, he said, to seeing the guardian of the nation’s soul shouted down by a mob hailing ‘the God Darwin and his prophet Huxley’ (Cohen, 1985).

‘Darwin . . . needed a champion as Huxley needed a cause’ (Desmond, 1994, p. 260) and long after the Oxford meeting, Huxley continued to fight Darwin’s fights with a razor intellect and acerbic wit, and although he was convinced by evolution, he was less convinced that natural selection was the mechanism. Much of Huxley’s motivation in defending Darwin was directed at reducing the power of the church and demolishing mutual enemies like Richard Owen. Huxley was an outstanding zoologist in his own right, and his expertise in anatomy

and palaeontology complemented Darwin's focus on natural history. Huxley also knew many of the leading scientists, including those in Germany responsible for new developments in anatomy, physiology and embryology (Nyhart, 1995; Richards, 2008). Like many of his contemporaries, Huxley was a polymath with a wide range of interests. He wrote on human evolution, produced a major work on the crayfish, and was fascinated by the recently discovered *Archaeopteryx*, devised an evolutionary classification of birds. On a broader front, Huxley championed education, and science education in particular, using his extraordinary communication skills, his talents as a blackboard artist and a restless energy to great effect. His commitment to the public understanding of science and his recognition of the value of combining teaching with research – as true today as it was then – is captured by this statement: 'The necessity of making things plain to uneducated people was one of the very best means of clearing up the obscure corners of one's mind' (Huxley, 1894).

On reading the *Origin of Species* Huxley's reaction was to say: 'How extremely stupid not to have thought of that!' (Huxley, 1900, p. 170). My aim in this essay is to provide an account, both historical and contemporary, of an area of biology Darwin failed to think of or possibly avoided: post-copulatory sexual selection. This was a topic that required a rather specific evolutionary outlook that did not become prevalent until the 1970s. Most of my own research in post-copulatory sexual selection has been on birds, and so I make no apologies for focusing largely, but not exclusively on this taxon.

## Origins of the origin

Darwin's ideas about evolution did not arise spontaneously. He had many antecedents, one of whom is John Ray (1627–1705), arguably the most perceptive naturalist of all time and who, in my opinion, has received insufficient credit (Birkhead, 2008). Ray changed the way we look at the natural world, and in doing so, provided the foundation for much of today's biology, including evolution. Ray's initial interest was in plants, but later decided with his tutee and friend Francis Willughby (1635–1672), to overhaul the entire field of natural history. Together, Ray and Willughby were part of the scientific revolution and produced the first scientific ornithology textbook in the 1670s. Their *Ornithology of Francis Willughby* (Ray, 1678) – so named because Willughby died in 1672 and Ray completed it alone – was a major step forward in zoology because it focused explicitly on evidence-based biology, rather than folklore. As great as it was, the *Ornithology* provides little indication of the monumental change in thinking Ray was later to bring about through a small volume entitled *The Wisdom of God*. (Fig. 1)

Before the late 1600s, most people believed that God had provided animals and plants for man's use . . . and abuse. The concept of physico-theology (known later as natural theology) presented by Ray (1691) in *The Wisdom of God* changed people's perception of the natural world. Physico-theology proposed that not only had God provided the natural world for man's enjoyment and edification, its perfection – the way

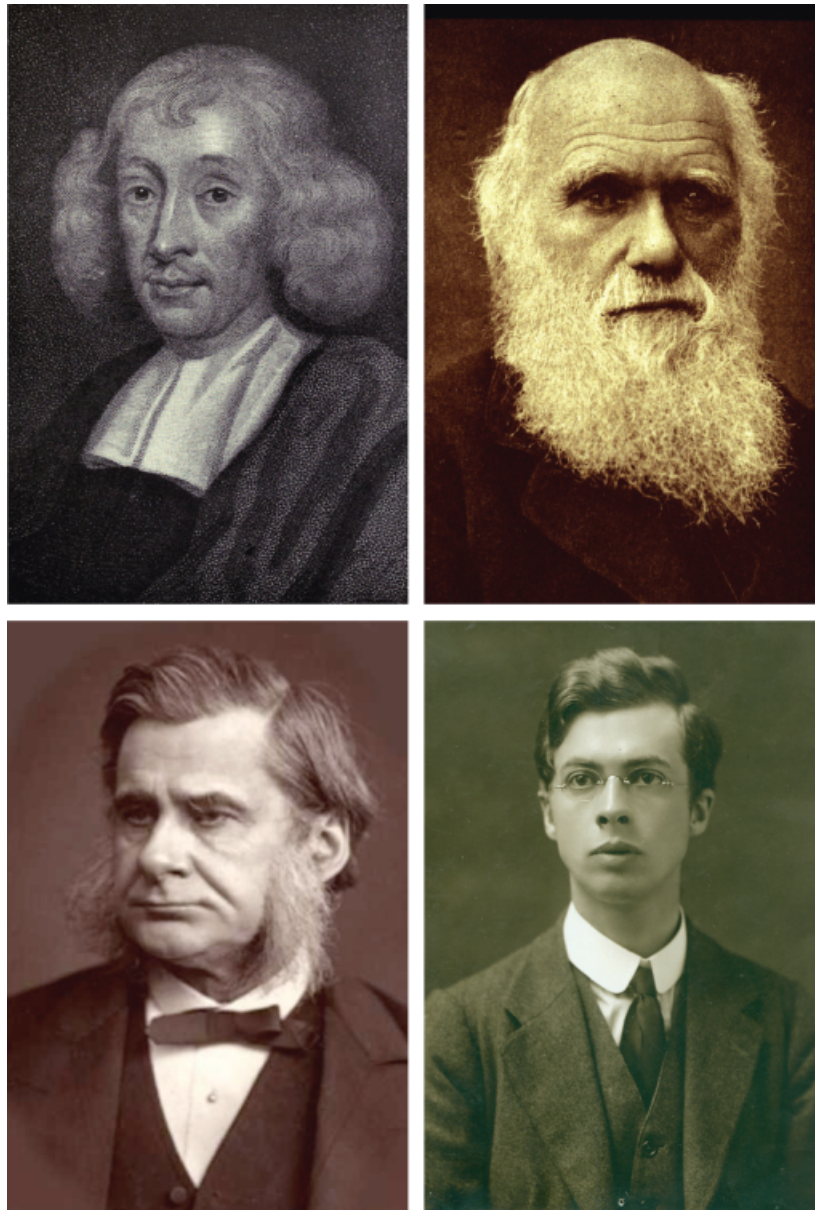
particular species seemed so well suited to particular environments – was evidence of God's existence.

In *The Wisdom of God*, Ray focused on ultimate causes, asking remarkably perceptive questions. Why, for example, do birds produce hard-shelled eggs instead of live young like mammals? Why do certain birds lay only a single egg, while others produce a clutch of ten or more? Why do different bird species have specific breeding seasons? These are questions that continue to interest biologists today. However, Ray did more than simply pose intriguing questions; he suggested answers, many of which – as subsequent research demonstrated – were extraordinarily accurate. Basically, Ray was interested in adaptations, and because he was a religious man, saw God as the mechanism by which they had arisen.

Physico-theology was extremely popular, so popular in fact that in the early 1800s, William Paley (1743–1805) borrowed extensively from Ray's book to produce his own version, entitled *Natural Theology* (Paley, 1802). An Anglican minister, Paley is best known now for his metaphor concerning the watch. 'Suppose I had found a watch' . . . he says 'its several parts are framed and put together for a purpose . . . the inference we think is inevitable, that the watch must have had a maker – that there must have existed, at some time and at some place or other, an artificer or artificers who formed it for the purpose which we find it actually to answer, who comprehended its construction and designed its use . . . The hinges in the wings of an earwig, and the joints of its antennae, are as highly wrought, as if the Creator had nothing else to finish. We see no signs of diminution of care by multiplicity of objects, or of distraction of thought by variety. We have no reason to fear, therefore, our being forgotten, or overlooked or neglected'. As is now obvious, Paley was the basis for the idea of intelligent design.

When Charles Darwin was an undergraduate at Cambridge studying for the church between 1828 and 1831, Paley's *Natural Theology* was required reading. Darwin loved it, later recalling that it provided: 'as much delight as did Euclid. The careful study of these works, without attempting to learn any part by rote, was the only part of the Academical Course which, as I then felt and as I still believe, was of the least use to me in the education of my mind. I did not at that time trouble myself about Paley's premises; and taking these on trust I was charmed and convinced of the long line of argumentation'. However, in his autobiography, Darwin subsequently wrote: 'The old argument from design in nature, as given by Paley, which formerly seemed to me conclusive, fails, now that the law of natural selection has been discovered' (de Beer, 1974).

Darwin owned a copy of the second (1692) edition Ray's *Wisdom of God* (Barrett *et al.*, 1987), and unlike many subsequent researchers, seems to have read it. The person whose ornithological ideas are most similar to Ray's, is David Lack (1910–1973), whose career was based largely on those same questions Ray asked – the evolution of clutch size and timing of birds' breeding seasons. Yet even Lack, who was so widely read, does not seem to have consulted *The Wisdom of God* (Birkhead, 2008). The most obvious



**Figure 1** Pioneers in biology: top left, John Ray (from Schuster & Shipley, 1917, courtesy of the Biodiversity Heritage Library), right Charles Darwin (courtesy of the Richard Milner Archive); lower left, Thomas Henry Huxley (Woodbury type print, Wikimedia Commons), and right Julian Huxley (Woodson Research Center photo files, courtesy of the Fondren Library, Rice University).

reason for this is simply the scarcity of the original. This is no longer an excuse because it is available online (<http://www.jri.org.uk/ray/wisdom/index.htm>).

Ray is exceptional not only for asking the right questions, not only for anticipating the right answers on many occasions but also for freely admitting that there were questions he could *not* answer.

Of the several key scientific events during Ray's lifetime, Antonie van Leeuwenhoek's discovery of 'animalcules' (spermatozoa) published by the Royal Society (of which Ray was a member) in 1678 was probably the most sig-

nificant. Ray incorporated Leeuwenhoek's extraordinary findings into a book on mammals (Ray, 1693), but was perplexed by Leeuwenhoek's speculation that only a single sperm was necessary for fertilization. To Ray, this simply did not make sense: 'The new opinion of Mr Lewenhoek [sic]. I am less inclinable to, because of the necessary loss of a multitude, I might say, infinity, of them [i.e. spermatozoa], which seems not agreeable to the wisdom and providence of Nature'. In other words, why would an all-wise God arrange for men and other male animals to produce millions of sperm if only one or a few were necessary for fertilization?

Ray (1691) was puzzled by another aspect of reproduction, asking: 'Why should there be implanted in each sex such a vehement and expugnable appetite of copulation?' I wonder whether there was a link between this question and the fact that in 1673, at the age of 45, Ray married a governess in the Willughby household, Margaret Oakley, some 25 years his junior (Raven, 1942).

In fact, there were several biological phenomena inconsistent with a wise and benevolent Creator, including the cruelty of cats playing with mice, the existence of internal and external parasites, of parasitoid insects, whose larvae consume their still-living host from the inside out. Religious fanatics found 'explanations' for such anomalies by suggesting that parasites were a form of punishment meted out by God, or as in Paley's case, that the positive aspects of life outweighed the negative ones.

Ray, however, in the true spirit of science, simply acknowledged that he could not account for the existence of so many sperm or that 'inexpugnable appetite' and that he would leave these questions for future generations.

Of course, the reason why Ray could not explain these particular phenomena was because they were incompatible with the conceptual framework of physico-theology. From Darwin's statement (above) about the superiority of natural selection over the argument from design, we might imagine that Ray's questions about reproduction would have been answered soon after the publication of the *Origin* in 1859. Not so.

## Darwin

Natural selection was, and still is, a better conceptual framework for thinking about the natural world, and provided a compelling and straightforward explanation for the existence of parasites and parasitoids. Sex, however, continued to be a mystery, and because Darwin largely avoided questions about the number of sperm and copulation behaviour, it was almost a century before anyone tackled these questions and offered a convincing answer.

Retrospectively, biologists such as Smith (1984, 1998) attributed Darwin's lack of interest in promiscuity to a statement in *Descent*: 'It is shown by various facts, given hereafter, and by the results fairly attributable to sexual selection, that the female, though comparatively passive, generally exerts some choice and accepts one male in preference to the others' (Darwin, 1871). The emphasis here being on *one* male, a clear indication that Darwin assumed females at least to be sexually monogamous.

I have suggested that Darwin made this assumption as a way of avoiding embarrassment, both with the public and within his family, especially his wife Emma and daughter Etty (Henrietta), the latter who helped him correct the proofs of *Descent* (Birkhead, 1997). Darwin's desire to avoid offending his family, undoubtedly reinforced by Victorian prudery, inhibited his writing on sexual matters. When he felt it necessary to discuss the sexual swellings of female primates, for example in *Descent* he wrote the passage in Latin knowing that Etty would be unable to read it.

Darwin was well aware of female promiscuity, from the literature, from his correspondents and from personal observation (Barrett *et al.*, 1987; Smellie, 1790). With reference to the pigeons he kept and bred, Darwin (1868) wrote: 'even when a male does break his marriage-vow, he does not permanently desert his mate'. Notice here that the emphasis is the male rather than the female breaking the marriage vow. Most pigeon breeders, however, including Girton (1765), whose book Darwin owned, recognized the existence of extra-pair copulations, pointing to the fact that selective breeding could easily be disrupted by a 'false tread' (an extra-pair copulation). Even more significantly, Darwin was aware of the extensive literature on so-called 'thief pigeons' in which particularly attractive males could cause paired females to abandon their partner in favour of themselves – even during the incubation period (Darwin, 1871; Birkhead, 2008). Darwin also knew that whatever it was that made these males irresistible to females was inherited, for pigeon breeders could select for it. Here was the best possible evidence for sexual selection, including female choice and female promiscuity, and yet for some reason, Darwin almost glossed over it. Thief pigeons are worth further study.

The second example of promiscuity was one Darwin (1871) cited in *Descent*. The information came from his cousin William Darwin Fox and involved the two species of geese he kept. In one season, a male Chinese goose seduced a white domestic goose, causing her to abandon her domestic gander: when the female's clutch hatched, it was immediately evident from the appearance of the goslings that both the Chinese gander and the white gander had fathered offspring: promiscuity and multiple paternity in a single, striking example.

With such clear evidence in front of him, it is easy (with the benefit of hindsight) to ask how Darwin could have overlooked the potential for promiscuity and sperm competition. In this instance, I think Victorian prudery won out over science (Birkhead, 1997), but Smith (1998) offers some other possibilities. He suggests that Darwin (and many of his successors) were psychologically predisposed to presume that females are monogamous. If so, the few explicit examples of female promiscuity that Darwin was aware of were then viewed as exceptions and could be ignored. Darwin may also have assumed pre-copulatory choice to preclude the necessity of female promiscuity. Finally, Smith (1998) suggests that during Darwin's lifetime, knowledge of sexual reproduction was both amorphous and confused, creating an intellectual barrier that prevented Darwin from considering the implications of female promiscuity.

As far as I am aware, there is no synthesis of what Darwin understood or did not understand about sexual reproduction in animals. He wrote extensively about the process of fertilization in plants, and so it is almost inconceivable that he did not have an interest in animal reproduction, and yet our understanding of Darwin's knowledge of sexual reproduction remains unclear. He knew a great deal about the reproductive anatomy of the barnacles he spent so long dissecting. We also know from his notebooks (Barrett *et al.*,

1987) that he had read Spallanzani's (1769) ingenious study from the late 1700s that erroneously concluded that spermatozoa had no role in fertilization. As Smith (1998) points out, Spallanzani's account of fertilization must have confused Darwin, and continues: 'Perhaps it was this confusion that pressed Darwin to his own fuzzy "gemmule" theory of inheritance [pangenesis], which despite its own vagaries at least restored a heritable male contribution to reproduction'. Smith then says: 'Ideas about fertilisation and heredity remained extremely amorphous through the eighteenth and most of the nineteenth centuries ...'.

While it is certainly true that ideas about heredity remained amorphous, it is less clear why Darwin should have remained confused about sexual reproduction. In *Variation*, Darwin (1868) makes clear that he was aware of relevant discoveries made during his own life time, including Prevost & Dumas' (1824) repeat of Spallanzani's experiment, which showed that spermatozoa were necessary for fertilization and Newport's (1851, 1854) confirmation that sperm enter the ovum, and the way this dictates the polarity of the developing embryo. Darwin (1868) was also aware of the prolonged sperm storage in certain insects (below).

There were other significant discoveries in reproduction that Darwin must (or ought to) have known of, including: (1) von Baër's (1827) discovery of the mammalian ovum and his later description of sperm-egg interactions in sea urchins (von Baër, 1847); (2) Wagner's (1837) documentation of the extraordinary diversity of sperm size and shape; (3) von Kölliker's (1841) discovery that spermatozoa need to make contact with the egg if fertilization is to occur; (4) rather later, Hertwig's (1876) demonstration that fertilization in sea urchins involves the fusion of male and female nuclei.

If he did not obtain it directly, Darwin's most likely conduit for this type of anatomical and physiological information is Thomas Huxley. Not only did Huxley receive lectures from some of the key players, like Thomas Wharton, describing the new German cell theory, fertilization and embryo development (Desmond, 1994, p. 26), Huxley later translated into English several major German zoology text books, including Kölliker's (1853) *Manual of Human Histology*, which contains a very comprehensive description of the male and female reproductive system, including this:

'Nor, from the experiments of Prévost, Dumas, Schwann, and Leukart, and the later researches of Newport ... can the least doubt be entertained that they [spermatozoa] are the true impregnating agent, and for the purpose of impregnation must necessarily come in contact with the ovum'.

Because Darwin had access to up-to-date information on sexual reproduction, including the processes of insemination, sperm function and fertilization, it seems at first sight unlikely that ignorance could account for his reluctance to explore the evolutionary implications of female promiscuity. On the other hand, if one reads the section in *Variation* (1868, p. 352) on sexual reproduction in relation to pangenesis, it is easy to see how Smith (1998) thought Darwin confused:

'The union of the two sexual elements seems at first sight to make a broad distinction between sexual and asexual generation ... [But] the now well-ascertained cases of Parthenogen-

esis prove that the distinction between sexual and asexual generation is not nearly so great as was formerly thought; for ova occasionally, and even in some cases frequently, become developed into perfect beings, without the concurrence of the male'. Yes – parthenogenesis must have been confusing.

'Why the [female] germ ... ceases to progress and perishes, unless it be acted on by the male element; and why conversely the male element, which in the case of some insects is enabled to keep alive for four or five years ... likewise perishes, unless it acts on or unites with the germ, are questions which cannot be answered with certainty. It is, however, probable that both sexual elements perish, unless brought into union, simply from including too little formative matter for independent development' [probably from Siebold (1857) – see Gregorio (1990, p. 756)].

Darwin continues:

'Quatrefages has shown in the case of *Teredo* [a ship worm], as did formerly Prevost & Dumas with other animals, that more than one spermatozoa is requisite to fertilise an ovum. This has likewise been shown by Newport who proved by numerous experiments, that when a small number of spermatozoa are applied to the ova of *Batrachians* [frogs and toads], they are only partially impregnated ...' [Jean Louis Armand de Quatrefages de Bréau (1810–1892): Darwin was clearly a fan because he had several of Quatrefages's publications in his library (for details, see Gregorio 1990)].

And finally:

'The belief that it is the function of the spermatozoa to communicate life to the ovule seems a strange one, seeing that the unimpregnated ovule is already alive and generally undergoes a certain amount of independent development'.

To conclude this section, the fact that Darwin believed several sperm were necessary to fertilize a single ovum should not have prevented him from seeing the evolutionary consequences of female promiscuity. However, focused as he was on his problematical theory of pangenesis – a theory Huxley urged him to reject – Darwin probably never made the intellectual leap that would have allowed him to identify the possibility of post-copulatory sexual selection.

## Individual selection

Until the mid-1960s, when natural selection was viewed explicitly in terms of individual selection, no-one did make that intellectual leap. On its own, however, individual selection may not have been sufficient: other factors may have contributed. The 1960s was a time of sexual liberation (Allyn, 2000), and biologists may have been motivated to explore areas that had previously been considered ethically inappropriate. From my own point of view, the best evidence that prudery continued to inhibit the study of sexual reproduction long after Darwin's day, and long after the 1960s, comes from two personal examples. First, when I decided to review the copulation behaviour of birds (part of the developing interest in sperm competition) in the mid-1980s, I was surprised to find that most published studies (spanning the previous 30 years) provided little detail,

appearing almost to avoid the topic, but whose authors were happy to provide details when asked directly. Second, after two of my female research students had given a talk on sperm competition in birds at the Edward Grey Institute student conferences in 2005, a senior scientist there commented how 'in his day' (i.e. the 1950 and 1960s) it would have been unthinkable of for a female researcher to talk about sexual processes in such an uninhibited way.

The shift in evolutionary thinking towards individual selection was mediated by the publication of George Williams' book *Adaptation and Natural Selection* (1966). Written in response to increasingly woolly thinking about the level (species, population, group vs. individual) at which natural selection operated, and given further impetus by the publication of Wynne-Edwards' overtly group selection *Animal Dispersion in Relation to Social Behaviour* (1962), Williams, together with John Maynard-Smith, and David Lack spearheaded a revolution in evolutionary thinking (Parker, 2006).

An explicit focus on individual selection changed the way certain biologists thought about sexual reproduction and revitalized Darwin's all-but-dead concept of sexual selection. Ironically, it was T. H. Huxley's grandson Julian Huxley who had previously sounded the death-knell for sexual selection in the 1930s. Huxley (1938) accepted the existence of male–male competition, but viewed it as an adaptation that allowed the stronger individuals to reproduce and hence benefit the species. As for Darwin's idea of female choice, Huxley (1938) simply dismissed it (Parker, 2006). Julian Huxley also reinforced Darwin's view about monogamy, and based on his observations of great crested grebes *Podiceps cristatus*, suggested that monogamy was the most harmonious (mating) system and one that humans should emulate (even though Huxley himself could not: Bartley, 1995). More ironically, Huxley (1912) was among the first to perform an explicit study of extra-pair behaviour in birds, but group selection thinking meant that his best interpretation of the forced extra-pair copulations he witnessed in mallards *Anas platyrhynchos* was that it was 'disharmonious'.

The key architects of the individual selection approach to sexual selection were Geoff Parker at Liverpool, and Robert (Bob) Trivers, then at Harvard, and their contributions are well documented (see Segerstråle, 2000; Alcock, 2001; Birkhead & Monaghan, 2010). Parker's approach comprised a mixture of theory and an impressive suit of empirical studies of sperm competition in yellow dungflies *Scatophaga stercoraria* (Parker, 1970, 2006). His paper *Sperm competition and its evolutionary consequences in the insects*, published in *Biological Reviews* in 1970, explained the evolutionary logic but also set out the agenda for future sperm competition studies. Trivers' initial contribution was mainly theoretical, although in the present context, the fact that some of his ideas were inspired by earlier studies of pigeon behaviour (Whitman, 1919) and by the pigeons outside his office window is significant because it demonstrated the feasibility of exploring the behavioural aspects of sperm competition in birds (Trivers, 1972, 2002) (Fig. 2).

Parker and Trivers were more than simply the architects of a revival of sexual selection; along with several others, they were also instrumental in developing the enormously

successful field of behavioural ecology (e.g. Krebs & Davies, 1978; Segerstråle, 2000; Alcock, 2001).

## Sperm competition

Parker's (1970) review paper, now a citation classic, considered the extraordinary adaptations to sperm competition in insects. The approach was male oriented, as was Trivers' (1972), largely because it was assumed that selection operated more intensely on males than females. It was a case of quantity versus quality: a promiscuous male could leave more descendants, whereas a promiscuous female could leave only better quality offspring. It was assumed that regardless of how many partners a female had, the number of offspring she produced would not change. The second reason for focusing on males was that male adaptations, whether they were behavioural, anatomical or physiological, were more obvious and more easily studied than female adaptations. There may also have been a cultural bias to focus more on males. When Trivers (1972) reported Bateman's (1948) ground-breaking work and used it to develop his theory of sexual selection in the late 1960s and the early 1970s, he presented only part of Bateman's results, ignoring those that indicated that females might benefit from copulating with multiple partners (see Arnold & Duvall 1994). When, in 2001, I quizzed Trivers about why he had done this, he told me unashamedly that it was pure bias. Trivers (1972) described Bateman's study in the following terms. Using genetic markers, Bateman (1948) measured the reproductive success of male and female fruitflies *Drosophila melanogaster*. For a male, the more females he copulated with, the more offspring he fathered (as a result of sperm competition), but for females, reproductive success did not change after she had copulated with one male regardless of how many other copulation partners she had had. In other words, females needed to copulate only once to fertilize all their eggs, but males benefited from being promiscuous.

However, Trivers did not reveal that part way through his experiments, Bateman had been forced to change the larval growth medium. Like a good scientist, Bateman kept the results separate, and those obtained when food was limiting for the fly larva actually showed that females did benefit, albeit not as much as males, from copulating with more than one partner. Trivers simply ignored those results. Interestingly, it was not until Arnold & Duvall (1994) went back and re-read Bateman's study that they realized what Trivers had done. Trivers (2002) himself has described how his 1972 paper came about, and more recently, Bateman's (1948) study has been reappraised (Snyder & Gowaty, 2007).

It was not until the 1980s that the idea that females might benefit from promiscuity came back on the agenda. In some ways, it may have been fortunate that Trivers and Parker first focused primarily on males because it meant that behavioural ecologists interested in post-copulatory sexual selection could investigate male function without the additional complexity of female biology. Had Trivers and Parker recognized at the outset that female processes were important, post-copulatory sexual selection would have seemed even more complicated



**Figure 2** Pioneers in post-copulatory sexual selection (top, left to right) Angus Bateman (John Innes Archives courtesy of the John Innes Foundation), Geoff Parker, Bob Trivers (lower, left to right) Randy Thornhill, Susan Smith, Bill Eberhard.

and might have deterred some researchers. As it was, behavioural ecologists were able to resolve many of the male aspects of post-copulatory sexual selection before beginning to address the female's role.

Although Parker and Trivers were key players in the development of behavioural ecology as a whole, the study of sperm competition itself was slow to progress (Simmons, 2001). This may have been because, initially at least, researchers thought that sperm competition might be peculiar to insects. My own involvement in this field started with an undergraduate lecture from Parker's colleague, R. R. Baker, in 1972, when I decided then that looking at bird behaviour, including sperm competition, from an individual selection perspective was what I would like to do. To others, birds with their predominantly monogamous mating system (Lack, 1968) seemed to be a particularly unpromising group in which to explore female promiscuity. However, I was fortunate to study guillemots *Uria aalge* for my PhD – a choice that was completely independent of any interest in sperm competition. During my background reading before going to Skomer Island, Wales, my study site for the next four summers, I could not believe my good fortune to discover a paper by a Danish biologist Nørrevang (1958), describing the high level of promiscuity in the guillemot. This, in turn, sent me looking further afield in the ornithological literature to see whether similar behaviour had been

recorded in other species. Indeed, it had: extra-pair copulation behaviour had been reported in a range of species, including the chaffinch *Fringilla coelebs*, Australian magpie *Gymnorhina tibicen*, rook *Corvus frugilegus* and certain ducks. Perhaps not surprisingly, these early observations were dismissed as non-adaptive; males were thought to be sick or have a hormone imbalance (Birkhead & Møller, 1992). With a group selection world view, or at least without an explicitly individual selection world view, extra-pair copulation behaviour did not make much sense.

Initially, the studies of sperm competition in birds focused largely on behaviour: copulation (between pair members but also with extra-pair partners) and mate guarding. Parker (1970) had drawn attention to the almost ubiquitous mate guarding behaviour in insects. An important issue here was timing: if extra-pair copulation and mate guarding were adaptive, then their timing was crucial. A key prediction was that mate guarding coincided with when a male's partner was fertile. This in turn raised the question of when females were fertile. This was less of a problem for insects, where prolonged sperm storage was well known, but the ornithological literature was curiously vague on this topic. The answer lay in forbidden territory for an ornithologist – the poultry literature. In the early 1980s, no self-respecting field ornithologist would admit to having an interest in poultry. Yet, much of my later research in sperm competition in birds

involved collaboration with poultry researchers, capitalizing on their enormous knowledge and ingenious techniques in reproductive biology. At the time, though, chickens and turkeys were not considered 'real' birds – rather they were the artificial product of thousands of years of domestication and selective breeding. But it was here that many of the answers lay, especially with respect to reproductive anatomy and physiology, including the period when a female could be fertilized, the so-called fertile period. In fact, it had been known for over two thousand years that hens could store sperm and produce viable offspring 2 or 3 weeks after her last copulation, later confirmed by poultry biologists who also showed the time course of fertility (Romanoff, 1960).

From the mid 1980s onwards, studies of sperm competition in more and more taxa started to appear, including mammals, fish, amphibia and different invertebrates. Smith's (1984) edited volume, the outcome of a prescient symposium he organized in Tucson in 1980, was a landmark, providing up-to-date information on all major taxonomic groups. The discovery of DNA fingerprinting as a way of detecting extra-pair paternity in birds (Burke & Bruford, 1987) transformed the field, and over the next decades, molecular methods for parentage assignment were developed for a range of taxa. Sperm competition studies progressed along two broad fronts. One made use of the new molecular methods to document the widespread nature of female promiscuity – eventually showing that true genetic monogamy was the exception rather than the norm among birds – and focusing on the adaptive significance of promiscuity (Griffith, Owens & Thuman, 2002). The other approach focused on mechanisms. I will deal with each in turn.

### **Adaptive significance of extra-pair copulations for males and females**

The adaptive significance of behaviour was the essence of the behavioural ecology approach and bird researchers were interested in the number of additional offspring a male fathered through his promiscuity. This question was more difficult to answer than initially expected because in order to measure male reproductive success it was necessary to assign paternity unambiguously (rather than simply identify genetic mismatches), and this was difficult both in terms of the fieldwork and the molecular methods. In the few studies where this has been done, some males do seem to father more offspring through their extra-pair activities, and of course, some lose paternity.

Much more difficult to answer was the question of the adaptive significance of extra-pair copulations for females. The male-biased view of extra-pair behaviour was transformed by a study of black-capped chickadees *Poecile atricapillus* in which Susan Smith (1988) showed that females actively sought extra-pair partners. This modest, observational study changed the way behavioural ecologists thought about extra-pair copulations, not just in birds, but in other taxa as well because it raised the possibility that in addition to making behavioural decisions about copulation partners, females might also have the ability to discriminate

between the sperm of different males. A flurry of studies followed, confirming that females of some species actively sought extra-pair opportunities (e.g. Kempenaers *et al.*, 1992) and raising the question that had so challenged Darwin about the possible benefits that females gained by choosing to copulate with a particular male. The issue was a thorny one in terms of extra-pair behaviour because the only benefits that females can gain are genetic, because (assuming extra-pair males provide no parental care – and typically they do not), the only thing they obtained from males was semen. The situation was very similar to that among the females of lekking species, where the only benefits of mate choice were indirect (genetic). Accordingly, this became known as the paradox of the lek (Kirkpatrick & Ryan, 1991). In fact, there was one direct benefit females could gain by copulating with more than one male – insurance against a partner being infertile. The idea among researchers that infertility might drive infidelity in non-humans is undoubtedly coloured by the situation in humans, where women are known to seek extra-pair partners if they are having trouble conceiving (Jequier, 1985). In birds at least, true infertility, that is, males having inadequate sperm supplies to fertilize a females' eggs, seems to be extremely rare (Birkhead *et al.*, 2008). Cases where we might expect temporary infertility as a result of sperm depletion, as in the case of polygynous species with particularly large harems (e.g. Gray, 1996), still need to be critically examined.

The lek paradox revolves around the maintenance of additive genetic variation in traits subject to strong, directional sexual selection (Fisher, 1930; Kirkpatrick & Ryan, 1991). If females prefer males with particular traits why have these traits not gone to fixation? Several solutions have been suggested, including fluctuating selection, such as that which would occur through host–parasite co-evolution (Hamilton & Zuk, 1982), and 'genetic capture' (Houle, 1992; Rowe & Houle, 1996), which is based on the idea of mutation–selection balance, where male quality of condition is determined by so many alleles that mutations occur as quickly as selection removes them. Testing these ideas has been problematic, for many reasons, but particularly because it has proved difficult to define and measure male quality.

It has also been suggested that the idea of females initiating extra-pair copulations in birds may have been overplayed (Westneat and Stewart, 2003). With no consensus over possible female benefits to promiscuity, it is possible (see Griffith, 2007) that for many birds, extra-pair copulation carries relatively little benefit, but also little cost, especially in those species where the incidence of extra-pair paternity is relatively low.

### **Mechanisms of sperm competition**

The first questions about the mechanisms of sperm competition now seem very basic: whether all female birds possess sperm storage tubules (Hatch, 1983) and whether relative testis size is a reliable proxy for the intensity of sperm competition. This latter idea was suggested by Short (1979) in a comparative study of primate testis size, although as

with so many ideas in biology, this had been anticipated much earlier by the extraordinary nineteenth-century Swedish biologist, Gustaf Retzius (see Birkhead & Montgomerie, 2009). In fact, the idea that relative testis size reflected promiscuity was recognized even earlier by John Ray and Francis Willughby in their encyclopaedia of 1676, wherein describing the European quail *Coturnix coturnix*, they stated: 'The cock has great testicles for the bigness of its body, whence we may infer that it is a salacious bird'. They were correct, and we now know that sperm competition is frequent in this species (Rodrigo-Rueda *et al.*, 1997). Willughby and Ray made the same inference as did Short, reasoning that large testes were associated with frequent male copulation. However, once Short had read Parker's (1970) early studies of sperm competition in insects, he recognized that rather than favouring male copulation frequency *per se*, it was female promiscuity that selected for both frequent male copulation and high sperm numbers as a way of males maximizing their likelihood of fathering offspring. Large testes produce sperm at a higher rate (Amann, 1970), and it is now clear that across the entire animal kingdom, relatively large testes are tightly linked to high levels of female promiscuity (Birkhead & Møller, 1998; MacLeod & MacLeod, 2009) and provide a useful clue to understanding mating systems.

A key question in the study of sperm competition was whether there were any rules that determined which of several males inseminating a female would fertilize her eggs? As related by Smith (1998), it was studies starting in the 1930s that were designed to control certain insect pest species by a sterilization procedure that identified both the widespread nature of female insect promiscuity and the fact that the sterile male technique could be used to investigate the outcome of promiscuity. By the 1930s, it was already known that the second of two males to inseminate a female generally fathered the majority of her eggs (Smith, 1984 and references therein). The sterile male technique was used by Parker to show that in his dungflies, the second of two males to inseminate a female in succession fertilized the majority (~80%) of the eggs (Simmons, 2001).

By coincidence, a similar pattern was apparent in birds. Starting in the 1920s, poultry biologists recognized that the last male fathered most offspring in females mated either naturally by two males in succession or artificially inseminated with semen from two males in succession. This phenomenon, in both insects and birds, was referred to as last male sperm precedence, or as P2 – the proportion of offspring fathered by the second insemination (Birkhead & Møller, 1992; Simmons, 2001).

What was the mechanism by which last male sperm precedence was achieved? Researchers were keen to answer this question as knowing something about the underlying mechanisms might shed light on other aspects of sperm competition. However, delving into the anatomy and physiology of reproduction was alien territory for most behavioural ecologists, many of whom had chosen behavioural ecology precisely to avoid more mechanistic aspects in their training.

For both insects and birds, researchers had proposed several potential mechanisms that would result in last male sperm precedence. The three main ones were: (1) displacement, where incoming sperm simply displaced previously stored sperm; (2) stratification, where the first inseminations were overlain by subsequent ones and a first-in-last-out system operated; (3) passive sperm loss, where second male precedence occurs simply because by the time the second insemination has occurred, some of the sperm from the initial mating may have been lost, passively, from the female tract, so that the second male's sperm are numerically dominant.

From the outset, Parker had used mathematical models to identify likely sperm competition mechanisms in insects, by evaluating both behaviour and physiological events associated with reproduction (Parker, 1984, 1998). Kate Lessells and I did the same in order to identify the most plausible mechanism of last male sperm precedence in birds (Lessells & Birkhead, 1990). We used what we thought was the most comprehensive dataset on last male precedence in the domestic fowl, from a study by Compton, Van Krey & Siegel (1978) in which hens were inseminated twice with equal numbers of sperm, 4 h apart, with sperm from the second insemination fathering 77% of the offspring. Modelling these data revealed that the most likely of the three mechanisms was displacement: the data were inconsistent with either stratification or passive sperm loss. Because displacement seemed intuitively unlikely in birds, I repeated Compton and colleagues' study, but found no evidence of a last male effect with inseminations separated by 4 h. However, experiments with a 24-h interval between inseminations did result in last male sperm precedence (Birkhead, Wishart & Biggins, 1995). In an attempt to establish why Compton and colleagues' results following inseminations separated by 4 h, differed from ours, it became apparent that our methods differed in a rather fundamental way. Compton and colleagues performed their first insemination soon after the female had laid (because it was assumed at that time that laying had no effect on sperm uptake), whereas our first insemination took place 7 h after laying precisely because my collaborator G. J. Wishart knew that inseminations soon after laying were less likely to be successful. The fact that we found no last male effect with an insemination interval of 4 h, but a pronounced effect with an interval of 24 h was consistent with the passive sperm loss model. Empirical studies later confirmed that passive sperm loss was responsible for last male sperm precedence in domestic fowl, turkey and the zebra finch (Colegrave, Birkhead & Lessells, 1995; Birkhead & Biggins, 1998). Indeed, on the basis of the similar way in which sperm are stored and utilized in all birds, it seems likely that passive sperm loss is ubiquitous in this taxon.

It is important to recognize that second or last male sperm precedence is not the *rule* in birds, especially in the wild. The experimental studies demonstrating the existence of last male sperm precedence in birds were conducted under very restrictive conditions, notably with equal numbers of equally competitive sperm in two inseminations. This is an unlikely scenario in the wild. Moreover, it is now known that both sperm numbers and sperm quality, which can vary substantially between males, have a marked influence on the

outcome of sperm competition (Birkhead *et al.*, 1999). In some species, males can allocate sperm number strategically (Cornwallis & Birkhead, 2006). It is also known that females can influence the uptake of a male's sperm, and so the outcome of sperm competition in the wild is likely to be a due to a combination of factors that can obscure or override the influence of insemination order.

Sperm competition mechanisms in mammals seem to be simpler than in birds or insects, probably because in most species, there is little or no sperm storage by the female and as a result, the interval between insemination and fertilization is usually much shorter, and sometimes just a few hours. An early, prescient model of sperm competition in mammals by Ginsberg & Huck (1989) proposed that the timing of insemination relative to sperm capacitation and that in turn relative to when the female ovulated would be crucial for the outcome of sperm competition. There is now good evidence for this and that the timing of capacitation varies between species (Gomendio *et al.*, 2006).

A particularly striking adaptation to sperm competition in rodents is 'sperm trains' – groups of sperm operating as a unit. The woodmouse *Apodemus sylvaticus*, for example, is a species with relatively large testes and high levels of multiple paternity (Baker, Makova & Chesser, 1999) in which sperm trains are typical. Moore *et al.* (2002) found that the curiously extended hook on the sperm head allowed sperm to grasp each others' flagella and swim as a 'train'. They also showed that trains swam faster than individual sperm, because their flagella beat in unison, and speculated that this sperm cooperation was an adaptation to sperm competition, allowing sperm to rapidly traverse the hostile vagina and enter the cervix, before moving individually to the site of fertilization. Later, in a comparative study, Immler *et al.* (2007) showed that sperm trains occurred in the ejaculates of other rodent species, and that the extent of curvature of the sperm head hook co-varied with relative testis size, providing clear evidence for a link between sperm design and the level of sperm competition.

In a follow-up to the Moore *et al.* (2002) study, Fisher & Hoekstra (2010) showed that even when two male *Peromyscus* mice inseminated a female in rapid succession, sperm formed trains predominantly with sperm from the same ejaculate, which is consistent with the theoretical prediction that sperm should cooperate only with closely related sperm. Sperm were even able to discriminate between sperm from their own male and sperm of a brother. Comparison with a monogamous mouse species in which sperm competition is absent showed that such discrimination is absent. This remarkable study provides additional evidence that sperm cooperation is an adaptation to sperm competition.

The mechanisms of sperm competition in insects are, as one might expect from their diversity of behaviours and morphologies, remarkably varied (Simmons, 2001). One of the simplest mechanisms, which occurs in dragonflies and damselflies, is sperm removal. In a pioneering study, Waage (1979) showed how male damselflies *Calopteryx maculata* use the hooks on their phallus, to remove previously stored

sperm from the female bursa and spermatheca before inseminating their own. In the giant water bug *Abedus herberti*, males copulate repeatedly with females as they are egg laying, and by doing so, fertilize the majority of eggs, even though the female has been inseminated previously by other males. The precise mechanism is not known, but it seems likely that by repeated insemination, the male ensures either that his sperm are closest to the point at which fertilization occurs, just as the egg is being laid, or are numerically dominant (Smith, 1979).

A particularly sophisticated form of sperm displacement occurs in the rove beetle *Aleochara curtula*. The male transfers sperm to the female in a spermatophore that, once the couple has separated, takes on a life of its own. A tube emerges from the spermatophore and enters the female's spermatheca, where its tip then inflates like a balloon completely filling the female's sperm store. The swelling spermatophore forces any previously stored sperm out of the store, before its own sperm are released, by two knife-like structures inside the female tract that puncture the 'balloon' (Gack & Peschke, 1994).

The mechanisms of last male sperm precedence in the yellow dungfly took rather longer to elucidate. Using detailed dissections and radio-tracers to follow the fate of sperm inside the female reproductive tract, Simmons and colleagues eventually revealed that when a male dungfly inseminates a virgin female, he deposits his sperm into the female's bursa, a bag-like structure connected to the spermatheca (the main sperm storage structure), by a narrow duct. Soon after insemination, a piston-like device sucks up the sperm, transferring it to the spermatheca. When the female copulates with a second male, the piston-like structure now acts in reverse, blowing out most of the previously inseminated sperm back into the bursa, before sucking up and transferring the sperm from the second male (Simmons, Parker & Stockley, 1999).

## Female processes

In the 1970s and the early 1980s the study of post-copulatory sexual selection was largely a study of male biology – indeed, the term 'sperm competition' tells us that the primary focus was on males. Behavioural ecologists were interested in females of course, but predominantly in terms of pre-copulatory sexual selection. This was because the evidence for female choice of partners was still extremely limited at that time. Because behavioural ecologists were focused on events occurring *before* copulation, Thornhill's novel suggestion in the early 1980s that females might make post-copulatory choices was virtually ignored. Thornhill (1983) referred to this process as cryptic female choice – cryptic because it took place out of sight inside the female's body – and proposed that under certain circumstances, it might pay females that had been inseminated by more than one male to discriminate between their sperm. The idea of cryptic female choice met with considerable inertia: the existing theoretical models did not take kindly to the idea of female control and the empirical barriers to demonstrating its occurrence were considerable. William Eberhard's

book *Female Control*, published in 1996, gave the subject a new impetus, documenting in encyclopaedic detail the range of possible mechanisms by which females could influence which of several males might fertilize her ova. Unequivocal evidence was still lacking, however, and to make matters worse, as often occurs in new areas of research, there was a surge of publications claiming – on the basis on very little evidence at all – to have demonstrated cryptic female choice. Similar band-wagon effects occur in all areas of science, partly because of genuine excitement about new ideas, partly because journal editors are keen to publish novel research and partly because few referees are competent to judge studies that span two or more disciplines. This is exactly what happened with cryptic female choice, rendering it vulnerable to the accusation of just-so story telling, as had occurred when new concepts in behavioural ecology first emerged (see Gould & Lewontin, 1979; Alcock, 2001). In an attempt to circumvent another ‘spandrels debate’, in the late 1990s, I listed what I considered the criteria necessary to demonstrate the existence of cryptic female choice (Birkhead, 1998). That paper generated some valuable discussion and helped to identify the main issue, which was that in order to demonstrate a female effect, one had to control completely for all possible male effects. This in turn made demonstrating cryptic female choice difficult, and encouraged behavioural ecologists to be ingenious in their experimental designs. Since then, there have been a number of studies, across a range of taxa, showing that females can influence which of several males fertilizes her eggs.

In a study of domestic fowl *Gallus domesticus*, Thornhill (1988) drew attention to the fact that females sometimes ejected semen shortly after they had copulated. Tom Pizzari and I later tested that idea using a free-ranging population of feral fowl that had been kept originally as pets at a research station in Sweden. Cryptic female choice via sperm ejection seemed plausible because male fowl sometimes copulate forcibly with females – and are able to do so because they are substantially larger than females. It is precisely in those instances where females have little pre-copulatory choice that we might expect post-copulatory mechanisms to evolve. As is well known, there is a dominance hierarchy or a peck order within groups of fowl, and we showed that females prefer to copulate with the dominant male. Subordinate males, however, are not passive and attempt to copulate with females whenever the opportunity arises, but females typically tried to avoid subordinate males by running away. When they were unable to do so, because they were caught and held by the subordinate male, they uttered a very distinctive distress call that immediately attracted the dominant male, who then attacked or chased the subordinate. Sometimes, however, the dominant male was either too far away to hear the female’s distress call or failed to respond, and the subordinate male was able to forcibly inseminate the female. When this occurred, the female very often ejected the male’s semen immediately their cloacae were disengaged and before the male had dismounted. In contrast, sperm ejection was rare following a copulation with the dominant male. To test whether females

based their sperm ejection on male dominance, we manipulated male social status, and confirmed that a change in male status was accompanied by a change in the likelihood of sperm ejection. In other words, through differential sperm ejection, females seemed to be able to bias sperm utilization in favour of the preferred male phenotype, in this case, socially dominant males (Pizzari & Birkhead, 2000).

Later, we were also able to show that female fowl can discriminate between sperm of different males with no information about male phenotype other than their semen. Using artificial insemination, and mixing equal numbers of sperm from two males, we found that certain females preferentially used the sperm of one male over another (Birkhead *et al.*, 2004). The mechanism by which females discriminate between the sperm of different males is not known, but an analysis of studies of interspecific hybridization in domesticated birds provides some clues and strongly suggests that immunological sperm–female recognition is involved (Birkhead & Brillard, 2007).

## Male–female co-evolution

While selection may favour male traits that increase the likelihood of fathering offspring with already-mated females, it is unlikely that females will be evolutionarily unresponsive to such selection. Any trait that increases a male’s fertilization success automatically reduces a female’s ability to control fertilization. For example, it may pay a male to have a long penis that enables him to place his semen at an optimal location within the female tract for fertilization. If females rely on post-copulatory events to determine which of several males fertilize her eggs, it will pay her to evolve traits that allow her to regain some control over paternity. In other words, under certain circumstances, we expect the co-evolution of male and female traits.

Such sexual conflict appears to occur in male and female seed beetles *Callosobruchus maculatus*. The male has a large spine-covered penis that punctures the female tract during copulation. This ‘copulatory damage’ may be a male strategy to deter the female from remating, thereby ensuring that the female’s eggs are fertilized by that male (Crudgington & Siva-Jothy, 2000). There is some evidence that females of *Callosobruchus* species whose males have a spiky penis have a thicker oviduct wall, than those without a spiky penis, suggesting correlated evolution between these two traits (Röön, Katvala & Arnqvist, 2007).

A better-documented example of male–female coevolution involves the relative size of sperm and the size of female sperm storage structures across a range of taxa including featherwing beetles, stalk-eyed flies, fruitflies, moths and dungflies and birds (see Pitnick, Wolfner & Suarez, 2009). That this correlation is due to coevolution has been elegantly demonstrated in *D. melanogaster* by Miller & Pitnick (2002) using an experimental evolution approach. By conducting sperm competition studies between males with relatively long or short sperm using females with relatively long or short sperm storage structures (sperm receptacles), these authors showed that the outcome of sperm competition was determined by an

interaction between sperm length and receptacle length, and that males with relatively long sperm were more successful in females with a longer sperm receptacle.

Another example involves waterfowl, renowned for their forced extra-pair copulation behaviour (McKinney, Derrickson & Mineau, 1983). Most ducks are socially monogamous, but the male plays little or no part in incubation or rearing the offspring. In some species, the sex ratio is male biased because of differential predation, and during the breeding season, the operational sex ratio (the ratio of sexually active males to fertilizable females: Emlen & Oring, 1977) is extremely male biased. Possibly, as a result, in many waterfowl species, forced extra-pair copulations are common, and can even result in the death of females, and so this is a costly activity for females (Huxley, 1912). Wildfowl are unusual among birds in that the male has a penis, and this may facilitate forced extra-pair copulations (see Montgomerie & Briskie, 2007). The waterfowl phallus is a remarkable structure; inactive, it lies coiled, inside out within a pouch inside the male's cloaca. The penis is basically a flat sheet of tissue, coiled when it is everted with an external groove along which the semen flows (Brennan, Clark & Prum, 2009). The penises of all waterfowl examined to date spiral in the same counter-clockwise direction away from the male (P. Brennan, pers. comm.). A comparative study of penis size in waterfowl found a positive correlation with relative testis mass, which is consistent with the idea that penis size evolved in response to post-copulatory sexual selection (Coker *et al.*, 2002). Given that forced extra-pair copulations are common, we might expect females to have evolved counter measures, enabling them to retain some control over fertilization.

A recent comparative study revealed the extraordinary reproductive anatomy of female waterfowl. In all other birds whose female reproductive anatomy has been examined, the vagina is a simple, tube-like structure (pers. obs.), but in different waterfowl species, the vagina may be branched, with blind-ending pouches and with a spiral-like design at the junction with the uterus. Strikingly, a positive correlation exists between the length of the phallus and the structural complexity of the vagina. Perhaps the most remarkable feature of the waterfowl vagina is that the vagina spiral is coiled in a clockwise direction from the male's perspective – that is, the opposite direction to that of the penis. Thinking back to earlier conceptual frameworks, both physico-theology and group selection would have struggled to make sense of this. An all-wise creator would surely have arranged for the two structures to spiral in the same direction, to facilitate insemination. Similarly, in a world in which evolution operated for the good of the species, it would be difficult to account for a pair of structures that so obviously did not fit together. Individual selection provides a convincing explanation for why the female's vagina should spiral in the opposite direction to that of the penis: to prevent forced intromission. So far, this is merely a hypothesis, and remains to be tested. I predict, however, that during pair copulations, the female relaxes her vagina, allowing intromission to occur, but during forced extra-pair copulations, by tightening the spiral,

penetration is prevented and the phallus is diverted into one of the blind-ending pouches (Brennan *et al.*, 2007). An interesting aspect of this study is that if the clockwise spiral of the female genitalia is an adaptation to reduce the likelihood of forced extra-pair fertilization, a mutant male whose phallus coiled in a clockwise direction (like the vagina) might be at a distinct advantage.

## Future

Paradigm shifts make science exciting, but once most of the major questions have been answered, a field is likely to decline in prominence. Sperm competition, to give the topic its original name, has endured for 40 years. Admittedly, the first decade was slow, but since then, the field has continued to grow. There are several reasons for this sustained interest. First, reproduction is the most fundamental activity organisms engage in. Second, sexual reproduction is complicated and there is much we still do not know. Third, post-copulatory sexual selection embraces many different areas of biology, from anatomy, behaviour, physiology and increasingly, genetics and molecular biology, generating new combinations of approaches. Fourth, new developments in various fields have the potential to help us better understand post-copulatory sexual selection. For example, fMRI brain scans and neurobiology will allow us to investigate previously unexplored aspects of promiscuity: does the prolonged copulation and orgasm that occurs (uniquely) in the red-billed buffalo weaver *Bubalornis niger* (Winterbottom, Burke & Birkhead, 2001), for example, generate similar sensations as occur in primates, including ourselves, during copulation? New techniques, such as the fluorescent labelling of live sperm from different males (e.g. Fisher & Hoekstra, 2010) and visualizing the way they interact within the female reproductive tract (Manier *et al.*, 2010), will change the way we view reproduction, literally.

The major unanswered question in post-copulatory sexual selection is the adaptive significance of female promiscuity. Over the past 30 years, behavioural ecologists have expended a huge amount of effort attempting to answer this question. There is no shortage of hypotheses and while many of the hypotheses individually have some support, absolutely no consensus has been reached regarding the adaptive significance of female promiscuity. It may be that there is no single explanation, but it is also possible that like John Ray, unable to explain his expugnable appetite or the multitude of sperm, that at present we simply do not have the right conceptual framework for thinking about female promiscuity. We may need a paradigm shift. It would be arrogant and naïve to think that there won't be one in this area, and when it comes and the truth behind female promiscuity is revealed, we too will say 'How stupid not to have thought of that'.

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