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selection it does contain a slight discrepancy. It is this: while it might pay males to sow their seeds widely and copulate with many different females, how could this be reconciled with the fact that females need to copulate only once? If the number of males and females are approximately equal how can most males copulate with many females and most females copulate with only one male? The presumed answer was that, as in Bateman's experiments, the females did copulate with more than one male, but reluctantly: they merely acquiesced. After females had copulated with one male, on being approached by another they lay back and thought of England, but their hearts weren’t in it. For a while at least this view of female behaviour satisfied most biologists but, as we shall see, it was flawed.

The Father of Sperm Competition

At the same time that Trivers was developing his ideas about sexual selection, Geoff Parker, now at Liverpool University, was thinking about one particular aspect of sexual selection: sperm competition. As an undergraduate at Bristol, Parker had been encouraged to study the behaviour of the yellow dungfly by the eminent entomologist Howard Hinton. As was true of many able students in those heady days in higher education, Parker was persuaded to continue this work for a Ph.D., still under Hinton's supervision. Only following a year of directionless study did Parker realize that if he was going to achieve anything he needed to address a specific question. After spending several months with his nose a few centimetres from fresh cowpats observing the intense competition between male dungflies for females, Parker recognized that the problem he should address was sexual selection - and specifically male-male competition. The issue was this: a female dungfly arrives at the cowpat ready to copulate and is then almost immediately ready to lay her eggs in the surface of the dung. She doesn't have to wait long, for as soon as she alights she is grabbed by a male, who instantly copulates with her. Before he has finished, however, a larger male grasps the pair, rips the first male from the female, discards him and copulates with the female. This scenario was enacted hour after hour, day after day, on every fresh dungpat. You can go out on a warm summer day and witness it for yourself: female dungflies routinely copulate with several males. Geoff Parker realized that when two males copulated with the same female during the same reproductive cycle they could continue to compete after copulation through the action of their sperm. Parker referred to this as sperm competition - a term that had been introduced previously by Otto Winge in 1937 to describe the same phenomenon in guppies. However, Parker was the first fully to appreciate the evolutionary significance of sperm competition, defining it as the competition between ejaculates of different males for the fertilization of a female's eggs.¹¹

Whereas Darwin's focus had been on the acquisition of partners, Parker's focus was on the acquisition of fertilizations. While Darwin assumed that gaining possession of a partner was sufficient, Parker pointed out that unless that male also fertilized the female's eggs, he would gain no genetic representation in the next generation. If sperm could compete for fertilizations within a female's reproductive tract, sexual selection would continue right up to the point of fertilization. By recognizing that sexual selection did not stop at insemination, and by combining this with what was then the new idea that what really matters in evolutionary terms is getting your genes into the next generation, Geoff Parker laid the foundations for the study of sperm competition. The essence of Parker's view was that if females copulated with more than one male, sexual selection would favour the males that fertilized most eggs. Males could win the fertilization contest by inseminating more sperm, by having faster-swimming sperm or by having sperm that disabled rival sperm. The way sperm win this contest is the basis for the study of sperm competition.

Parker's view of evolution, which had its roots in the work of George Williams and John Maynard Smith, among others,¹²
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was that selection operates on individuals rather than on populations or species as a whole. This individual-based view of evolution got its first major airing with the publication of E. O. Wilson's groundbreaking volume *Sociobiology*, published in 1975, and the next year was popularized by Richard Dawkins in *The Selfish Gene*. Implicit in Parker's ideas about sperm competition was the notion that far from being a co-operative venture between the sexes, reproduction was a selfishly motivated exercise, with each male and female out to maximize their benefits and minimize their costs. Sometimes the interests of each sex coincided, creating the illusion of cooperation, but most of the time each individual was out to get the best deal - even at the expense of his or her partner. This is sexual conflict: the battle of the sexes, where males and females are out to screw each other for the best, selfish genetic deal they can get. As we shall see, this unconsciously selfish attitude by each sex has been the driving force for many behavioural, physiological and anatomical aspects of reproduction.

Interestingly, for reasons that will become clear, Parker was initially less concerned with the battle between the sexes, than the battle within one sex: between males. Perhaps the most fundamental point Parker made about sperm competition was that it generates opposing selection pressures for males. On the one hand, sexual selection favours those males who successfully fertilize females who have previously been inseminated by other males. On the other, it simultaneously favours those males who prevent females they have inseminated from being fertilized by any other male. The benefits of securing fertilizations with additional females are considerable: more offspring bearing copies of that male's genes. But the costs of being cuckolded are also considerable. The reproductive success of a cuckolded male is depressed. And it can be reduced even further if, like ex-UK Prime Minister Harold Macmillan, cuckolded by Lord Boothby, a male spends time and energy rearing offspring that are not his own - frittering away resources that could have been used to promote his own genes or secure reproductive success elsewhere. In the light of this it is ironic that Macmillan was famous for the phrase 'You've never had it so good.'

The outcome of the conflicting selection pressures created by sperm competition is the evolution of traits that promote male reproductive success. It is an evolutionary arms race. As soon as males evolve some character, such as a larger ejaculate, which increases their success, there is counter-selection on males better to protect their paternity, through, for example, behaviours that reduce the perceived likelihood of female infidelity. As soon as such behaviour has become effective, there is counter-selection on males to find another way to circumvent this.

Geoff Parker is indisputably the father of sperm competition. Multi-talented – he is also a jazz musician and breeder of champion chickens – Parker has been described recently as the 'professional's professional'. His ideas from the late 1960s and early 1970s provided the basis for all subsequent research in this field. Not only that; over the past thirty years he has continued to expand this theoretical base and construct a conceptual superstructure around which empirical tests of his ideas have been performed. Layer by layer, year by year, the subtlety and complexities of post-copulatory male competition continue to be revealed.

**Had Darwin Thought of Sperm Competition?**

In almost all his voluminous writings Charles Darwin assumed that females were monogamous and copulated only with a single partner in each breeding attempt. Bob Smith of the University of Arizona, who edited the first compendium on sperm competition published in 1984, accused Darwin of delaying the study of sperm competition because he assumed females to be monogamous. Was Darwin really that naïve? Like his grandfather, Erasmus, Darwin was aware that sexual reproduction was the principal source of variation on which natural and sexual selection worked to cause evolution. Moreover, both Erasmus and Charles had read Spallanzani's *Essay on Animal
Reproduction of 1769, in which the process of fertilization was first inferred. Given Darwin's recognition of the importance of sexual reproduction, it is hardly surprising that during his brainstorming years following the return of the Beagle he should have recorded in his notebooks many aspects of reproduction, including infidelity in chickens and multiple paternity in dogs. Later, Darwin had a protracted opportunity to think about sperm competition—in barnacles. Darwin's eight tedious years of barnacle dissection were enlivened by two discoveries. The first was that not all barnacles were hermaphrodite; some species had separate males and females. But, and this was the second revelation, in many species the males were minute with several living parasitically inside a single female. Stunned by his discoveries, Darwin wrote and told his friends. To Charles Lyell, his geological mentor, he described the situation in one particular species:

...the other day I got the curious case of a unisexual, instead of a hermaphrodite, cirripede [barnacle], in which the female had the common cirripedal character, and in two of the valves of her shell had two little pockets, in each of which she kept a little husband; I do not know of any other case where a female invariably has two husbands...

In other barnacle species Darwin found as many as fourteen miniature males inside a single female. These findings were so extraordinary that much of his barnacle monograph is concerned with convincing his readers that these diminutive and rudimentary organisms really were males of the same species and not parasites. Darwin described them as mere bags of spermatozoa and in discussing their general biology made an implicit statement that both or all males inside a particular female could potentially fertilize her eggs. Subsequent barnacle studies have verified the accuracy of Darwin's observations and speculations, although it still remains to be shown the extent to which the sperm from the different males within a single female compete to fertilize her ova.

After completing his barnacle volumes, Darwin decided in 1855 to breed pigeons. As anyone who has kept them will know, pigeons provided Darwin with an excellent opportunity to observe courtship and reproductive behaviour at close range. And in a throwaway line in his rarely cited book on Domestication, Darwin provides one of the first ever references to extra-pair behaviour in male birds: 'Pigeons... can be easily mated for life, and, though kept with other pigeons, they rarely prove unfaithful to each other. Even when the male does break his marriage-vow, he does not permanently desert his mate.'

Perhaps the most explicit of all Darwin's statements regarding sperm competition appears in his volume Sexual Selection and the Descent of Man. The information originated from his cousin, William Darwin Fox, rector at Delamere in Cheshire. Fox kept a menagerie of farmyard animals, which over the years provided him with numerous observations and anecdotes for his cousin. Fox recounts that he had two types of goose: a gander and three female common geese and a pair of Chinese geese. The two types of goose had kept quite separate until one year the Chinese gander seduced a female common goose. When the eggs of this female hatched, it was clear from the appearance of the goslings that four of the eggs had been fathered by the common gander, the other eighteen by the Chinese male. So, as Darwin wrote: 'The Chinese gander seems to have prepotent charms over the common gander.' A clearer observation of sperm competition would be hard to find.

Darwin also knew about the potential for sperm competition in humans. When he wrote to his life-long colleague Joseph Hooker, who was on a botanical expedition in Bhutan, to tell him about the supplemental males in barnacles, Hooker wrote back acknowledging that Darwin's barnacle discoveries were wonderful. But, he said, they paled into insignificance in comparison with the polyandrous humans he was encountering, where 'a wife may have 10 husbands by law'. In their racy biography of Darwin, Adrian Desmond and James Moore interpret this as Hooker drawing a parallel between primitive
people and primitive animals, both lacking the virtues 'innate to Gentlemen of the highest Victorian class'.

With so much evidence for sperm competition staring Darwin in the face, why didn’t he pursue the idea within his framework of sexual selection? One possibility is that he simply never made the connection. In a riposte to my suggestion that he had falsely accused Darwin of delaying the development of sperm competition, Bob Smith proposed that Darwin failed to recognize the magnitude of its evolutionary implications. However, given Darwin's perceptive ideas about most other areas of biology this seems unlikely. It is much more plausible that Darwin was inhibited. Victorian values made it unacceptable for someone in his position to discuss the nitty gritty of animal reproduction. It was admissible to discuss fertilization and illegitimacy in plants, as Darwin did, but the line between plant and animal sex was a rather clear one. Earlier, in the seventeenth century, sexual reproduction was discussed openly, and even in the late 1700s it was still acceptable and fashionable for Grandfather Erasmus to be a libertine. His monumental poems on the reproduction of plants were highly acclaimed by contemporary critics, although (or perhaps precisely because) they were little more than thinly veiled erotica. But by the time Charles was writing about sexual selection things had changed dramatically and Victorian prudery was well established. Thought to have arisen as a consequence of the Industrial Revolution and the rise of capitalism, the Victorian repression of sex was seen as a way of controlling the masses, preventing them from dissipating their energies and permitting them to do only what was essential to maintain the workforce. Whatever its cause, sexual repression made it difficult for Darwin to discuss animal reproduction. Darwin's thoughts were not repressed, however, and it was only in those writings he assumed would be read by the susceptible masses themselves that he avoided discussing animal sex. Because he doubted whether anyone other than broad-minded academics would ever read his barnacle volumes, which were rather technical, they are refreshingly frank when it comes to reproductive anatomy. Darwin describes with uninhibited enthusiasm the penis of one species being 'wonderfully developed', lying 'coiled up, like a great worm' and when 'fully extended, it must equal between eight or nine times the length of the animal'. Elsewhere in these volumes he discusses other aspects of barnacle genitalia and spermatozoa, terms that never saw the light of day in his more popular books.

In a sense this omission is hardly surprising since, as its title implies, *The Descent of Man and Selection in Relation to Sex* was ostensibly a book about Man, despite the fact that more than half the book is concerned with other animals. Had he so much as breathed a whisper about competing sperm, his readers would soon have put two and two together and made six. In fact, Darwin probably never stood a chance of discussing any sexual topic in much detail because his wife Emma and more particularly his hypochondriac daughter Henrietta acted as his censors. Darwin was sixty when he wrote *Descent*; he was slowing down and willingly handed over some of the responsibilities of correcting proofs and refining the text to his daughter. Henrietta has been described as both a closeted Victorian matriarch and a fussy moralist and it seems likely that she exerted a powerful force over what was and what wasn't morally acceptable in her father's books. As well as editing *Descent*, she gave Darwin's biography of Grandfather Erasmus the once-over, slashing out the bits she felt were unsuitable, including Charles's statement regarding his grandfather's 'ardent love of women'. Some idea of Henrietta's outlook on the world can be gauged from the fact that she initiated a campaign to eradicate the stinkhorn fungus, whose scientific name, *Phallus impudicus*, at once describes it and explains why she felt the sight of one might be a bad influence.

Ironically, it was, I suspect, the ghost of Erasmus Darwin that provided the ultimate deterrent and prevented Charles from developing any ideas he might have had about sperm competition. Erasmus was obsessed by sex, both in theory and in
practice. At a theoretical level he was well aware of the value of sexual reproduction in creating variation. On a more practical note, he prescribed it to his patients as a cure for hypochondria. But far worse from the family's point of view, Erasmus had fathered illegitimate children. The family had always known about this, but precisely at the time Charles was writing *Descent*, sixty years after his grandfather's death, rumours were circulating about the widow of a friend being an illegitimate granddaughter of Erasmus. Any discussion of sperm competition, however dispassionate, could very easily have backfired, and the subject was therefore left well alone.20

A Battle within a Battle of the Sexes

So far our focus has been on males and on sperm competition. This is deliberate. However, recall that I mentioned briefly that early in the history of sperm competition it was recognized that selection operated on each sex separately and how, in evolutionary terms, each sex was designed to maximize its own reproductive success. But — and this is a very significant ‘but’ — this battle between the sexes was seen as a very asymmetric one with active males and virtually passive females. Males fought for females; males displayed to females; males inseminated females, and their sperm then battled to fertilize a female's eggs. The most females were thought to do was to choose between different partners. This view, prevalent throughout the 1970s, appeared to be little changed from one proposed by Walter Heape in 1913.21

The Male and the Female individual may be compared in various ways with the spermatozoa and ovum. The Male is active and roaming, he hunts for his partner and is an expender of energy; the Female is passive, sedentary, one who waits for her partner and is a conserver of energy. To the Male it is the sexual act which is of moment, while it is the consequence thereof which profoundly affects the Female.

This androcentric view of reproduction goes back to Aristotle, and despite Darwin's ingenious idea about female choice, sexual selection was still a male-dominated process. This gender bias, which stemmed from a mixture of unconscious sexism and biological ignorance, persisted and formed an important part of Parker's and Trivers's formulation of sperm competition. However, Parker did at least provide a biological reason for his male-orientated vision. It was this: a male who copulates with, and fertilizes, as many females as possible (including some previously inseminated by other males) will produce more descendants than one who does not do so. For a female, however, copulating with more than one partner is unlikely to increase the number of offspring she produces; the best she can hope for is an increase in their quality. Parker's view was based on the idea that evolution is a game of numbers — what counts is how many genetic representatives an individual has in subsequent generations — and because quantity is more important than quality, sexual selection operates more intensively on males than on females.22

The basis for this argument was female passivity, the idea that females simply acquiesced. This view may have been an accident of the fact that the first sperm competition studies were conducted on insects, animals so far removed from ourselves that it was difficult to tell what their motivation was. It was not until the 1980s when researchers started to look at sperm competition in vertebrates, and in birds in particular, that it was realized that, far from being passive, females often actively sought multiple male partners. With this realization there was a major shift in the emphasis of research. If females choose their partners, and if they actively choose to copulate with several males, might they not also choose between the sperm of different males? Just as sperm competition had been a continuation of pre-copulatory male–male competition into a post-copulatory context, so sperm choice was a continuation of a female's pre-copulatory choice of a sexual partner. Moreover, as soon as it was recognized that females might choose
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between the sperm of different males, it was clear that there
would be conflict between the sexes. Whenever one sex, let’s say
it is the male, constrains the reproductive success of the other,
selection immediately favours an adaptation in females to
overcome the constraint. The result is sexual conflict — the
battle of the sexes — and an escalating arms race of adaptation
and counter-adaptation between males and females. Put simply:
sperm competition + sperm choice = sexual conflict.

It is probably no accident that the increased interest in female
aspects of behavioural ecology, including sexual selection,
coincided with the continuing expansion of the feminist move­
ment. Bob Smith told me that when the book on sperm
competition he edited was published in 1984 his chapter on
sperm competition in humans triggered off an angry response,
particularly among militant feminists. The feminist movement
in North America in the 1970s was epitomized by a popular
bumper sticker, attributed ro (he journalist Gloria $teinem,
which read: ‘A woman without a man is like a fish without a
bicycle.’ For women who didn’t need a man at all, the idea of
having several to induce or facilitate sperm competition was
anathema.

This story also reflects how female academics interested in
sexual selection on opposite sides of the Atlantic differed in
their approach to the gender bias in behavioural ecology.
Without doubt, the most radical feminists were (and still are)
North Americans. By contrast, those in Europe adopted a much
more subtle, and ultimately probably a more persuasive,
strategy in their efforts to change the way (male) biologists thought
about reproduction. Moreover, it is important to recognize that
amending the gender bias has not been an entirely female
prerogative; several male behavioural ecologists have actively
promoted the female perspective. It is unfortunate, therefore,
that these include several who continue to be, until recently at
least, targets of North American feminist criticism.

In terms of recognizing the importance of the female per­
pective we have come a long way in the thirty years since sperm
competition was first identified as a component of sexual
selection. Some feminists might still argue that we have not
come far enough, but the majority of behavioural ecologists I
talk to think that the balance is now reasonably even. Despite
this substantial shift in outlook, research effort over the past
few years has done little to change the view that sperm choice
and the interactions between sperm competition and sperm
choice are often extremely subtle and remarkably difficult to
elucidate. As we shall see later, this is exemplified by the
difficulty behavioural ecologists have had in identifying both
the mechanisms by which females control the paternity of their
offspring (chapter 6), and the adaptive significance of polyandry
itself (chapter 7).

Reproducing Controversy

Like many new areas of science, the combined field of sperm
competition and sperm choice stimulated a huge amount of
innovative research. Indeed, it is recognized that one of the main
ways in which science makes progress is through a set of new
ideas resulting in a fundamental change in outlook. This is
referred to as a paradigm shift44 and for those involved it is one
of the most exhilarating aspects of science. Paradigm shifts are
characterized by intense excitement and high productivity,
followed, as things settle down, by a period of what is referred
to as ‘normal science’. Depending on the magnitude of the shift
and the type of science involved, the initial phase of enthusiasm
and productivity may last months or years. Paradigm shifts
might be the engine that drives scientific discovery, but at the
same time they are open to exploitation via what I call ‘the
bandwagon effect’. The wave of enthusiasm for a fashionable
new area of research creates an opportunity, utilized by some
researchers, for the publication of hastily conceived and poorly
executed research, thereby allowing them to jump aboard the
bandwagon.45 This process is facilitated by two factors. First,
new areas of research have, by definition, few experts capable of