Males typically go to great lengths to impress females and ward off competitors for mates. For humans, think flowers, diamonds, fast cars, and the old phrase about the relative efficacy of candy and liquor. A diversity of approaches is not unusual. Some birds have taken this competition to yet another level, and one remarkable example is the ruff (Philomachus pugnax). Ruffs are wading birds that breed in the Palearctic tundra. In spring, the males, adorned with flashy black and brown breeding plumages, meet in mating arenas called leks. Every fighter looks different from its rival, like a population of domestic cats. One hypothesis is that their extremely variable plumage is used in social interactions, so that males can recognise each other and establish an energy saving hierarchy that prevents unnecessary fights between unequal opponents on the lek. The plumage therefore could serve as a silent song, since ruffs have no need for an elaborate display song.

Leukking ruff males fight vigorously for the right to mate with smaller, plain-looking prospecting females. Although not necessarily a question of life and death, these fights are not just to put on a good show, since males occasionally draw blood from their opponents. The winner, the most dominant male, will get the lion share of matings, the others must be content with the leftover, less fussy females. Arguably, the Latin name Philomachus (battle lover) or the German name Kampfläufer (fight runner) describes these peculiar birds more accurately.
Both the German and Latin names fail to capture the variation in the species though, because the taxonomists didn’t know better. But in this case, the failing is dramatic. Over the last decades, behavioural biologists have discovered that not all ruffs are born as fighters. Around 1 in 7 are ‘Satellite’ males, which can be readily identified because they sport fancy white plumage ornaments on leks. Satellites display without getting involved in fights. They form a temporary uneasy alliance with a territorial male on his small court, and remain there because they help to draw in females who visit the lek. They are not directly rewarded by their ally, which looks odd at first glance because they make him more attractive to the other sex. Satellites are crafty though. They are masters in using the confusion that frequently arises during the many conflicts between lekking fighters to mate quickly with females.

To make things even more interesting there is also a third type of male that remained unknown until ten years ago. They dubbed this new type ‘Faeder’, an Old English word for ‘Father’. Faeder males are cross-dressers: small males that don’t grow ornaments or perform elaborate male displays, but rather resemble females in appearance and behaviour. Because of this, behavioural biologists did not distinguish them from females for a long time. The ringers proposed that this was the ancestral type of ruff male and that ornamented males evolved from this form at a later stage. Faeders are the smallest morph, but given the strong size difference between the sexes in ruffs, these males are still bigger than the largest female. Big is beautiful, so these cross-dressers can appear very attractive in the eyes of a territorial male. Faeders use stealth and distraction tactics to obtain matings. They hang around on the lek, and when a receptive female crouches to signal its willingness to mate, they move quickly to be the first to mount her. As a second tactic, the Faeder may convincingly take on the female copulation posture himself to divert an ornamented male away from the female. This is a very effective distraction, although you might say that Faeder males pay a fair cost since they are themselves frequently mounted by the love-seeking Fighters.

During previous studies we found that the three male morphs have parallel female equivalents, and that offspring inherit their morph type from both of their parents. To find out exactly what genes control development into the three types, we teamed up with other geneticists at University of Sheffield and sequencing experts from University of Edinburgh, and compared the DNA sequences of Fighters, Satellites and Faeders. This study revealed that the three morphs differ only in a small part of DNA sequence located on chromosome 11, comprising less than 0.5% of the genome. The differences originated from a ‘chromosomal inversion’, a rare event where one chromosomal part flipped by 180°. This profoundly changed the local chromosomal structure and the destiny of the approximately hundred genes that are located in the inverted fragment. The flip made recombination for this stretch of DNA nearly impossible, meaning that the gene variants are trapped together and evolve together, in isolation from the rest of the genome, accumulating new mutations and therefore slowly turning into new variants. The initial event caused Faeder males to lose their ornamental plumage and their elaborate male display behaviour. A Swedish and Chinese research group, who worked in parallel on describing the DNA
differences between the three morphs, dated the emergence of the inversion to about 4 million years ago.

Satellites and Faeders each have their own inversion variants. The Satellite variant is a derived form and looks like a hybrid between Fighter and Faeder. It probably arose through a highly unlikely exchange of genes between chromosomes of the original and Faeder versions through another adaptive recombination event that happened around 500,000 years ago. During this exchange, the Satellite variant assimilated intact copies of some genes to restore plumage ornaments and display behaviour.

Inversions are not unique to ruffs. They were first described in fruit flies about a century ago. These changes to chromosomal structure provide the perfect substrate for evolution of new forms. The sex chromosomes are full of them and the many differences between males and females are due to these simple re-arrangements. With the rise of genome biology, geneticists have learned that chromosomes are far from being the static macromolecules that classic genetics had previously suggested. For example, classic cytogenetic marker studies only identified nine inversions that differ between humans and chimpanzees, whereas the full genomic sequences revealed that there are now already around 1,500 described. Approximately 90 to 125 genes are found in the inverted region of the ruff. Many of these genes will be responsible for the known and unknown differences between the three morphs. Most eye catching are the genes that encode proteins for steroid metabolism, because these hormones are known to be involved in regulating aggressive behaviour. The most prominent candidate gene for aggression differences is called non-spectacularly HSD17B2 (or hydroxysteroid-17β-dehydrogenase-2 by its full name). It may hold the key to explain hormonal differences between males during the breeding season. Previous functional studies have shown that HSD17B2 converts testosterone, which is tightly linked to aggression in many species, to the weaker androgen androstenedione. Strikingly,
during the breeding season male Fighters have relatively high levels of testosterone and low levels of androstenedione whereas the two non-aggressive male forms, Faeders and Satellites, show the opposite pattern. You may have already guessed it: Faeders and Satellites also carry different variants of this gene from the one of the Fighters. These variants have two large deletions around this gene, meaning that parts of the DNA sequence are simply missing without a replacement. Therefore this gene may be differently regulated in the two morphs carrying the inversion, which could impact development and expression of aggression. Because steroids are often affecting many more genes, this change may impact multiple genes, those that affect aggressive behaviour but also others, that affect traits responsible for the development of display plumage and behaviour, and body size.

Although simple, the genetic re-arrangement does have a dramatic effect on life expectancies of ruffs. The inversion shared by Faeders and Satellites breaks up a gene that encodes an essential cell division protein called centromere protein N. No eukaryote can survive without at least one intact copy of this gene, meaning that all Satellites and Faeders are heterozygotes - carrying one intact and one broken copy of this gene. When analysing the offspring of crosses between inversion carriers we also found that having only one good copy increases mortality of young ruffs. This means that the inversion has severe costs on its bearers. How has it not gone extinct by natural selection then? A hint perhaps comes from comparing the size of testes of ruffs. Satellites and Faeders have much larger testes and therefore may be better in sperm competition, which is rife on ruff leks, since most females mate with more than one male. As Satellites and Faeders have larger testes, they may be releasing more sperm, and so stand a better chance at fertilising the female's egg. Another possibility is that the exhaustive competition with its associated stress on leks shortens the life expectancy of the Fighter males, so that their survival advantage during the juvenile stage turns into a disadvantage during adulthood.

The lekking system is one of the most extreme forms of sexual selection. A lot of Fighters would give a lot to have more stress during the breeding season, since the leks serve only the crème de la crème of the Fighters and the females visit the leks to be able to choose from the very best. But most Fighters will never obtain a court on the lek. These marginal ruffs may spend years floating around and searching for the rare opportunities to join a lek and to reproduce. We currently don't know whether this is also true for Faeders and Satellites. Perhaps on average a Satellite or a Faeder has a higher chance to have offspring than a Fighter? Being born as an inverted ruff would then not be such a bad idea after all, if they can manage to survive the first year. The discovery of the genetic differences provides us with the tools to start such investigations in wild populations and discover how the three morphs, which evolved following a random genetic event in the distant past, can coexist in nature today.