Chapter 14
Sexual Selection: Following Darwin's Legacy

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Abstract Much of the knowledge we treasure about evolution, and biology in general, rests on Darwin's ideas about sexual selection put forward 150 years ago. In his work *The Descent of Man, and Selection in Relation to Sex*, Darwin posited two fundamental mechanisms of competition for reproduction: intrasexual competition and mate choice. Since then, we have come to understand that, along with these two mechanisms, competition over reproduction also depends on sperm competition and cryptic mate choice. In this chapter, we review what we have learned about these four mechanisms and discuss general aspects about the sex roles, the evolutionary battle between the sexes, and the overall relevance of sexual selection for our understanding of the natural world. After 150 years of studying sexual selection, today we know that with this idea Darwin not only completed the general outline of his Theory of Natural Selection, but also laid the foundations of what has become one of the most complex and stimulating fields in the study of evolution. A vital process to understand not only the evolution of males and females, but also the processes of speciation, the ability of populations to adapt to changing environments, or the evolution of sexual reproduction itself.

Keywords Evolution · Sexual selection · Animal behavior · Sexes

14.1 Introduction

Parson's chameleon (*Calumma parsonii*) is one of the most spectacular reptiles on the planet. This chameleon is not only striking for its size (currently recognized as the heaviest chameleon species), but also for the imposing rostral protuberances of males (Fig. 14.1). Such protuberances have been described in other chameleons, where they range from subtle supranasal lobes to prominent antlers. In the case of beetles of the family Lucanidae, which includes the iconic stag beetle (*Lucanus*

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Fig. 14.1 Males of *Calumma parsonii* (left), *Calumma oshaughnessyi* (top) and *Furcifer willsii* (bottom). Photographs by Roberto García-Roa

cervus), males of some species possess such hypertrophied mandibles that they can be longer than an adult female. In birds of paradise (Paradisaeidae), males sport very distinct finery in the form of conspicuous plumage colourations accompanied by a variety of feathery structures, such as plumes, wires, or diadems. In addition, the males of these species usually exhibit sophisticated dances that, to the sound of their attractive melodies, combine colour and movement in one of the most amazing spectacles of nature. The males of some species take meticulous care even of the scenery for these dances, as is the case with the Western Parotia bird of paradise. In this species, males choose a clearing in the forest and spend hours cleaning it of branches and leaf litter to ensure the perfect staging for their dance.

These are just a few examples of the kind of traits that challenged the Theory of Natural Selection as Darwin (1859) formulated it in *The Origin of Species* (*Origin* from now on). In a world supposedly dominated by competition for survival, how to explain the evolution of such extravagant and apparently costly traits for the survival of organisms? This question was a real headache for Darwin, as he reflected in a letter to his friend the American botanist Asa Gray: “The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick!” (3 April 1860, letter DCP-LETT-2743).

In *Origin,* Darwin devoted a few paragraphs to speculate on the role of those phenotypic traits in males that could be used as weapons in the battle for reproduction (Darwin 1859). However, it was not until 1871 when, in his book *The Descent of Man* (*Descent* from now on), Darwin formalized sexual selection as a process that could explain the evolution of what he called secondary sexual characteristics [following Hunter 1837]: the “armaments” for combat that he had alluded to in *Origin* and the “ornaments” that had so obsessed him, such as the intriguing feathers of the peacock (Darwin 1871). In essence, Darwin described sexual selection as a process analogous to natural selection, but where competition between individuals of the same species occurs over reproducing more and/or with the best available mates.

One hundred and fifty years after the publication of his work (Darwin 1871), we know that Darwin was right: the display of colour, sound and movement of males in birds of paradise seeks to captivate females (Diamond 1986), the jaws in stag beetles are used as tools with which to dislodge potential mating competitors, and the rostral protuberances of chameleons seem to play an important role both in male-male combat and in seducing females (Karsten et al. 2009; Emlen 2014). Indeed, sexual selection has turned out to be a central evolutionary phenomenon for understanding evolution along the tree of life, and it is underpinned by the same principle that Darwin formulated 150 years ago: the variability of heritable traits involved in competition for reproduction (Darwin 1871). What Darwin could never have guessed is the extraordinary complexity and sophistication of the different mechanisms of sexual selection, a labyrinth of processes that all emanate from that apparently simple but devilishly intricate principle, competition for reproduction.

14.2 Pre-copulatory Mechanisms: Darwin's Jigsaw Puzzle

In *Descent,* Darwin explains sexual selection on the basis of two mechanisms that in turn reflect two types of competition for access to mating. First, competition between individuals of the same sex (usually males) through adaptations that increase their success in confrontations with other competitors (e.g. armaments), either by intimidating or reducing the opponent. An example of this is the aforementioned jaws of the stag beetle. Second, competition between individuals of the same sex (usually males) to be more attractive to the other sex, which chooses suitors through a phenomenon known as mate choice. For example, the choice by female birds of paradise for those males with more showy displays (e.g. ornaments).

14.2.1 Intrasexual Competition: Fighting for Mates

Intrasexual competition occurs when there is a direct confrontation between individuals of the same sex for access to mating. It should be noted that this type of competition occurs in both males and females. However, and for reasons that we will discuss later, in general terms it is much more intense among males, something that Darwin already recognized in *Descent*:

> [. . .] it is, with rare exceptions, the male which has been the more modified. [. . .] The cause of this seems to lie in the males of almost all animals having stronger passions than the females. Hence it is the males that fight together and sedulously display their charms before the females (Darwin 1877, p. 221).

Thus, intrasexual competition explains the development of adaptations such as the large antlers on the males of some ungulates (or the serrated femurs possessed by the males of some species of sucking bugs). These adaptations have evolved because

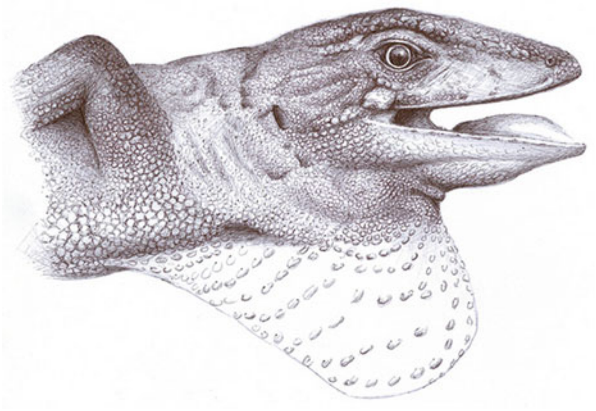

Fig. 14.2 *Anolis wermuthi* showing its gular crest. This behaviour is typical in this genus of lizards and seeks to intimidate possible competitors during social interactions. Drawing by Frutos García García

they increase reproductive success when in direct confrontation with individuals of the same sex (Andersson 1994).

Although the ultimate goal is clear, access to mating, the way to achieve it varies between species. For example, combat between males can occur with the aim of dominating one or more females (a harem), as in the case of lions. On the other hand, competition may be for dominance of a good territory, one with ample food sources, water, a wide range of hiding places or other resources important to the species. Better territories will attract more females to mate with (i.e. *resource-defence polygamy*).

Intrasexual competition sometimes involves physical contact that can become very violent. Fights are usually not deadly, but they can be harmful even for winners. Because of these costs, intrasexual competition does not usually involve combats. Evolution has endowed males and females with different mechanisms for assessing the quality of their competitors, and thus weighing the costs/benefits of escalating combat. As a result, confrontations are usually ritualized and only sometimes (when there is no clear winner in the ritualized phase) become fierce fights. Striking colourations, extravagant morphological structures and displays are some of the most common mechanisms that seek to intimidate and discourage the opponent before direct contact is made (Andersson 1994). In this process, evolution has favoured phenotypic traits that are good indicators of competitive quality. For example, males of the genus *Sitana* lizards display the extensible fan of skin they possess in the throat area (called the “gular fan”) in order to signal vigour in front of other males (Kamath 2016). The gular fan is involved in the social interactions of many species of lizards, such as American lizards of the genus Anolis (Fig. 14.2) or Asian lizards of the genus Draco. Thus, by means of this type of structure, males minimize the costs of their confrontations. In fact, in species with extreme armaments (e.g. venomous snakes), fights never fully escalate and are fundamentally ritualized.

14.2.2 Intersexual Competition: Mate Choice

In addition to directly, through ritualized and/or fierce combat, individuals of the same sex may compete with each other, indirectly, to see who is more attractive to potential mates. Darwin called this phenomenon "intersexual competition" because selection occurs via the opposite sex, through "mate choice". In mate choice, evolution will tend to favour those individuals who find attractive traits that are good indicators of benefits associated with their potential mate, which we classify as direct and indirect (Andersson 1994; see Edward and Chapman 2011).

We speak of direct benefits when choice is made on the basis of material resources (Andersson 1994). For example, males may collaborate in parental care (or even take care of it exclusively), serve as protection against other males or predators, offer nuptial gifts (e.g. nutrients transmitted before or during copulation), or a good territory (e.g. with ample food resources, hiding places and/or low parasite density). We call these benefits "direct" because they translate into a greater investment of resources for offspring. In the spinach fish (*Spinachia spinachia*), for example, males fan their nests to improve oxygen flow to the eggs. This increases hatching rate and, consequently, reproductive success for both parents. In this species, females prefer males that perform stronger flapping and body shaking during courtship, which serve as indicators of their parental quality (Östlund and Ahnesjö 1998).

In contrast, we speak of indirect benefits when choice has to do exclusively with effects that derive from the genes that the offspring will inherit from the couple. That is, the benefits here have to do exclusively with improving the quality of offspring. Indirect benefits result from inheriting genes that, on average, will be different from those inherited if females randomly mated (i.e. they are not the result of a greater investment in resources). Different models have been proposed to explain how mate choice may have evolved based on these types of benefits. According to the *good genes* model, females benefit from mating with males whose genes increase the viability of their offspring (Möller and Alatalo 1999). By viability here we mean genes that increase an individual's ability to survive, such as its ability to flee predators, metabolize nutrients, etc. According to this model, selection will favour the evolution of preferences for those traits that are good indicators of viability, so that the underlying genes are inherited by offspring.

Alternatively, Fisher proposed that secondary sexual characteristics may evolve because they are attractive to females per se, known as the "*sexy sons*" model (Fisher 1930). Let's say that a preference for a particular trait arises in a population. For example, a preference for long caudal feathers in males because these increase flight efficiency and, therefore, offspring viability. Since females carrying the genes "for" such preferences will mate with males carrying the genes "for" long tails, the two will tend to be transmitted together. If the preference in females is for "longer" tails, a process of directional selection (*runaway selection*) will be initiated, where traits are exaggerated generation after generation even beyond the point where they are no longer advantageous for flight, but costly. This process explains the evolution of traits that can compromise survival, simply because carriers with more exaggerated traits have greater reproductive success (Kirkpatrick 1982). In fact, this process of rampant selection will only cease when the costs in terms of survival are equal to or greater than the benefits of being "sexy". Fisher's model could explain the appearance of such extravagant traits as the peacock's tail.

14.3 Post-copula Mechanisms: The Invisible Competition

From the second half of the twentieth century onwards, the definition of sexual selection expanded as we understood that this process transcends mating. On the one hand, because the development of molecular techniques shows that polyandry (i.e. a female mates with more than one male in the same reproductive cycle) is very common in the animal kingdom (Arnqvist and Nilsson 2000). On the other hand, because data accumulate from species in which females have specialized structures that allow sperm storage for prolonged periods of time (e.g. Holt and Lloyd 2010). The sum of these two factors sets the scene for the war over reproduction to continue after mating, in the reproductive tract of females, through sperm competition (Simmons 2001) and cryptic choice (Eberhard 1996).

14.3.1 Sperm Competition: Fighting for Fertilization

Since the number of eggs a female can produce is limited, evolution will favour any adaptation that allows males (i.e. their sperm) to fertilize more eggs than their competitors (Parker and Pizzari 2010). This postcopulatory competitive mechanism was described in insects by Geoff Parker, who called it "sperm competition" (Parker 1970). Fifty years later, thanks to the use of molecular techniques, we know that this phenomenon occurs in a multitude of vertebrates and invertebrates (Smith 2012). For example, in many species males modulate the amount of sperm with which to inseminate females according to the number of competitors. Since sperm production is not costless (Parker and Pizzari 2010), evolution favours those males able to optimize their sperm investment according to the number of opponents. Increasing the number of matings with the same female and predicting her peak fertility are mechanisms that also favour the success of males in fertilization (Smith 2012). In addition, sperm motility and viability, as well as other characteristics of the ejaculate, are crucial in sperm competition (Smith 2012).

In addition, males may adopt strategies that prevent or reduce the competition that their own sperm will face within the female reproductive tract. For example, males of some species escort females during and after mating to prevent them from being inseminated by competitors, a behaviour called "mate guarding". A classic example is dragonflies (Fig. 14.3), where males may remain attached to females for extended periods of time to prevent females from re-mating (Alcock 1994). One need only

Fig. 14.3 Dragonfly mating (Belgium). Photograph by Roberto García-Roa

look closely at a pond in spring to see tandems of dragonflies flying, with the males clinging to the females by means of genital *claspers*, until females stroke the surface of the water to deposit their eggs there. The variety and elaboration of adaptations for sperm competition is extremely diverse, from structures that allow them to "sweep away" the ejaculate of their opponents, as in the case of the mealworm beetle *Tribolium castaneum*, to nuptial plugs that are anchored to the genital opening of the female after copulation to make it difficult for other males to insert their sperm (Andersson 1994).

14.3.2 Cryptic Female Choice

The role of females in postcopulatory competition is not limited to serving as a battleground for sperm competition. In many species, females play a decisive role in the competition for fertilization. Polyandry gives them the opportunity to favour the sperm of the males that confer the greatest benefit to them. This process was termed "cryptic mate choice" by Thornhill (1983) and involves a variety of morphological, physiological or behavioural mechanisms (Eberhard 1996). For example, females can avoid full intromission of the penis of lower quality males, thereby reducing the amount of ejaculate inseminated. They may also terminate copulation earlier or prevent mating males from displacing the sperm of previous males (Eberhard 1996). Even after successful copulation, females may bias the use of one male's sperm by discarding the sperm of others, by transferring unselected sperm to locations where another male could displace it, or simply by storing the sperm of the preferred male so that it is the one that preferentially fertilizes her eggs. Females may also vary offspring production depending on the male they mate with, ceasing ovulation and/or egg maturation, failing to prepare the uterus for development, or even aborting when mated with an unwanted male (see Eberhard 1996).

14.4 Sex Roles and the Evolutionary Battle of the Sexes

Darwin observed that, while males of most species were willing to copulate frequently, females were more cautious (Darwin 1871). As we have seen above, sexual selection tends to be more intense in males: either directly through intrasexual competition or indirectly through mate choice. In 1948, geneticist Angus John Bateman used the vinegar fly (*Drosophila melanogaster*) in an attempt to understand this widespread principle (Bateman 1948). In his work, Bateman concluded that, while females achieved their greatest reproductive success after only a few copulations, that of fervent males increased linearly with the number of matings. He suggested that, compared to males, females were more constrained in the number of offspring they could produce. This essentially has to do with anisogamy, whereby female gametes are much larger and more expensive than male gametes. This greater investment in a smaller number of gametes means that females tend to have a potentially much lower reproductive rate than males. This, in turn, has conditioned the evolution of parental care and, in general, of investment in offspring, favouring divergent reproductive strategies; the so-called "sex roles" in males and females (Trivers 1972; Lehtonen et al. 2016). Thus, while selection tends to favour the evolution of strategies that maximize the number of females males mate with, in females it tends to favour strategies that maximize the quality and survival of their offspring. As a consequence, males tend to vary much more than females in their reproductive success (i.e. there is a greater difference in reproductive success between the best and the worst male in a population than between the best and the worst female). This, in turn, implies that sexual selection acts much more intensely on males, as often only the few best males monopolize access to females. Although this paradigm has many exceptions (e.g. species with reversed sex roles), this general trend holds true throughout the tree of life (Janicke et al. 2016).

An unsuspected consequence of the existence of sex roles in nature is that the sexes often have different ways of maximizing reproduction. In fact, the evolutionary interests of males and females rarely coincide, so that their fitness cannot be optimized simultaneously (Parker 2006). This phenomenon, known as "sexual conflict", is associated with intense competition between males and often triggers an arms race (i.e. antagonistic co-evolution) between the two sexes (Arnqvist and Rowe 2005) that Dawkins referred to as "the evolutionary battle of the sexes" (Dawkins 1976). Sexual conflict has received increasing attention in recent years, to the point of being recognized today as one of the main phenomena of sexual selection. First, because it is essential for understanding why males and females respond as they do to sexual selection. Second, because it can act as a driver of biodiversity, favouring processes of inter-population evolutionary divergence and even speciation (Gavrilets 2014). Third, because it can have very negative consequences for populations. For example, in response to intense sperm competition, males of some insect species have evolved genitalia with spines that cause considerable damage to females during mating. Such male harm increases female investment in reproduction in the short term (by diminishing their future survival) and reduces female re-mating, thus increasing the reproductive success of the male, but at the expense of the female (Parker 2006). Similarly, *D. melanogaster* males transfer a "sex peptide" in their ejaculate that manipulates females to lay more eggs in the short term and reduce their receptivity to other males, again at the expense of their longevity and their own fitness (Wigby and Chapman 2005). Spiked genitalia and toxic ejaculates are but examples of how high levels of competition between males (i.e. intense intrasexual competition) can result in adaptations that, while serving to compete effectively against other males, in doing so harm females, reducing their fitness (Parker 2006). Male harm to females is not only extraordinarily widespread in nature, but can lead to a "reproductive tragedy of the commons" where sexual conflict can drastically reduce a population's capacity for growth and viability, even to the point of extinction (Rankin et al. 2011).

14.5 The Importance of Sexual Selection in Evolution

Throughout its different eras, the Earth has witnessed an infinite number of adaptations, of sounds, colours, morphologies and behaviours (Darwin 1859). Many of these adaptations have been sculpted by sexual selection, one of the two pillars of Darwinian evolution. Based on competition for reproduction and fertilization (Andersson 1994), sexual selection has become a cornerstone for understanding the evolution of adaptations in males and females and, ultimately, for understanding the history of life on earth. Sexual selection is a fundamental driver of speciation processes (Panhuis et al. 2001). For example, the extraordinary adaptive radiation of birds of paradise, whose elaborate courtships and ornaments we have already discussed, is largely due to the runaway action of sexual selection (Ligon et al. 2018). Moreover, sexual selection is also a determinant process for the viability of species and their populations, for their ability to adapt to changes in the environment (Pomiankowski and Moller 1995). We now know that sexual selection is a powerful mechanism that purges the genome of deleterious mutations (Radwan 2004), which protects populations against inbreeding depression, a key phenomenon in extinction (Lumley et al. 2015). Indeed, sexual selection is such an effective evolutionary mechanism that it often dominates natural selection.

First, secondary sexual traits favoured by sexual selection tend to be closely linked to traits with direct impact on the condition of their carriers, including traits that directly influence the average fitness of the population, such as survival (e.g. anti-predator abilities, ageing), fecundity, or the quality of their offspring (e.g. parental care). Today we know that the expression of complex armaments and ornaments depends to a large extent not only on the inheritance of certain alleles "for" these traits, but also on the general condition of the organism, its overall "genetic quality". Thus, sexual selection tends to select genotypes with generally good combinations of traits, most of which need not be directly linked to reproduction, in a process called "genic capture" (Rowe and Houle 1996).[1] Second, because sexual selection is more intense in males than in females, it is an extraordinarily efficient evolutionary mechanism because most of the costs of selection are paid by males, the non-reproductive sex. In other words, at the population level, the best genes are filtered out (genic capture) at the cost that many males do not leave offspring, while most of the females in a population do reproduce. This selective filtering tends to increase average population fitness, and considerably increases the speed at which it evolves and, therefore, its ability to adapt to sudden changes in the environment. This is especially true in reference to directional and sustained environmental changes, such as climate change. These evolutionary advantages possibly explain why the overwhelming majority of animals, plants and fungi reproduce sexually even though, at first glance, it seems more costly than asexual[2] reproduction.

14.6 Conclusions

We still have a long way to go, a long list of challenges in the study of sexual selection that undoubtedly hide great discoveries to be made. For example, we still do not fully understand the evolution and characteristics of mate choice preferences. We still ignore basic aspects related to the distribution, variability and shape of preference functions, the costs associated with choice, or the role of the social environment and the cognitive mechanisms involved in mate choice (see the chapter by Santos and Varela in this volume). Likewise, we have paid too little attention to intrasexual competition in females or to the evolution of sex between individuals of the same sex, both phenomena that are much more widespread than we suspected. Nor do we understand well how sexual selection operates in complex environments, subject to the environmental variations that are characteristic of most habitats in which organisms reproduce in nature. Most of the advances we have made to date in

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[1] Genic capture is one of the processes that could resolve the Lek paradox, since most of the phenotypic variability in the expression of secondary sexual characteristics would not be directly linked to genetic variability in the alleles directly responsible for the expression of secondary sexual characteristics, but to the general condition of the individual which, in turn, would condition the development of these characteristics (Rowe and Houle 1996).

[2] An asexually reproducing organism transfers all its genes to its offspring (not just half) and reproduces twice as fast as a sex-differentiated organism (where one of the sexes does not reproduce), known as the "*two-fold cost of sex*" (i.e. Smith 1971; Smith and Maynard-Smith 1978).

the field of sexual selection have focused on studying the mechanisms of sexual competition in stable environmental conditions, such as those of the laboratory, and therefore we are far from understanding how these discoveries translate to nature. Another major challenge is to understand what factors are determinant in the evolution of sexual conflict, why this phenomenon, so widespread in nature, results in damage to females in many species and not in others, and what consequences it has for population viability. It will also be crucial to fully explore the role of phenotypic plasticity in secondary sexual traits, and how such responses can give rise to feedbacks between ecological and evolutionary processes; fundamental both for understanding how sexual selection operates and its role in adapting to the increasing demands of change that challenge this planet's biodiversity.

In short, we have come a long way since the publication of Darwin's second and often forgotten masterpiece, his massive *Descent* in 1871. Probably because Darwin devoted the main title and much of this book to human evolution, it may give the impression that sexual selection is a secondary aspect of this work. On the contrary, Darwin's ideas on sexual selection are undoubtedly the main contribution of this book to the study of evolution, and to the study of biology in general. By presenting his ideas on sexual selection 150 years ago, Darwin not only completed the general outline of his theory of natural selection, but also laid the foundations of what has become one of the pillars of evolutionary biology. A field that, since the 1970s of the last century, has exploded to reveal itself as one of the most complex and exciting in the study of evolution. What better testimony to Darwin's second greatest idea?

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