

Chapter 6

Beyond Coy Females and Eager Males: The Evolution of Darwin's Sexual Selection

Thierry Hoquet

To a biologist, the meaning of sex is complex. In a general sense, “sex” designates any process of genetic recombination [1]. This broad definition also applies to lateral transfer of genes in bacteria and viruses and is not restricted to reproduction. A narrower definition of biological sex for vertebrate animals is directly linked to reproduction. A third meaning is associated with sex as reproduction: it signifies a distinction between “two sexes”: “males” and “females”. But what are the “sexes”, and on what grounds should they be distinguished: merely morphological (males and females differing in their internal and external appearance), gonadic (i.e. based on the possession of testes or ovaries), or genetic (males and females being endowed with two different sets of chromosomes)? Sex as reproduction and sex as the sexes are two different concepts, but they are closely related in the biological scheme, as the most general (and minimal) criterion that biologists use to define the sexes is that “males” make small gametes while “females” make larger gametes—both gametes being involved in sexual reproduction. But a definition invoking production of gametes is conventional and there are exceptions (especially among non-vertebrate living beings) [2]. According to this technical definition, in vertebrate animals the two sexes are equated with two types of gametes or reproductive cells: “the smaller of the two gametes is called a sperm and the larger an egg”, which does not mean that “sperm” come cheap [3].

Sexual selection is the concept that Darwin devised to account both for human racial divergence and for sexual dimorphism or the difference of aspect between individuals of the two sexes, males and females. Darwin was struck by the fact that some traits could not have been shaped by natural selection, as they were likely to be detrimental to the survival of their bearers, being wasteful in terms of resources and energy and making their bearers more conspicuous or vulnerable to predators: brightly coloured plumages in birds or exuberant singing in frogs may attract

T. Hoquet (✉)

Faculté de Philosophie, Professor of Science History
and Philosophy, University Jean Moulin, Lyon, France
e-mail: thierry.hoquet@hotmail.fr

predators as well as potential mates. Sexual selection argues that what an individual loses in terms of lower probability of survival may be more than compensated by increased probability of having more couplings or attracting better mates. In modern understandings of biological processes, there is no essential reason to distinguish sexual selection sharply from natural selection: sexual selection is part of natural selection, both contributing to the fitness of the individual and leading to a greater transmission of its hereditary units (genes).

This paper starts with an analysis of Darwin's argument and seeks to understand how sexual selection has suggested different models for the behaviours of males and females, following what I call the "two-sex" hypothesis: the idea that the study of animal behaviour should follow a divide between two different strategies. The two-sex hypothesis suggests that males and females have different strategies, namely, that (1) all males act in the same way (promiscuously) and (2) all females act in the same manner (choosiness). This applies to all males (or females), both within one species and in any species considered. The alleged universality of sexual selection theory is clearly evinced in a milestone paper by A.J. Bateman, where he states that, in non-hermaphrodite organisms, "there is nearly always a combination of an indiscriminating eagerness in the males and a discriminating passivity in the females", a statement that is said to apply to *Drosophila* and to "derived monogamous species (e.g. man)" [4].

More recently, theoretical attempts have been made to overcome the two-sex hypothesis. Whether or not one agrees that there are two sexes in nature (i.e. two types of gametes), one may challenge the idea that all sperm-producers or all-egg producers, whatever their species, should behave according to the same patterns. This paper shows how sexual selection theories developed away from the two-sex hypothesis to more gender-neutral models: where the analysis of reproductive tactics pays more attention to interspecific and intraspecific differences in behaviour; and where success is increasingly explained not by mating strategies but by taking into account time allocation and random encounters between individuals.

Starting with Darwin's theory, this paper emphasises its male-centred biases, often explained away by the fact that his views were obscured by the prejudices of the Victorian era. In contrast, other social contexts, like the sexual liberation and sex equality movement of the 1970s, triggered strong criticism of male chauvinism in biological theory and paved the way for new models and observations. Accordingly, this paper focuses on the development of sexual selection theory, especially by showing how feminist biologists in the 1970s–1980s have led sexual selection away from stereotypical sex notions, such as "eager" males and "coy" or "monogamous" females.

6.1 Darwin's Sexual Selection

The concept of sexual selection has always been a powerful vector for myths of sex and gender, based on the assumption of a two-sex dichotomy. On the basis of Charles Darwin's work, two mechanisms were put forth under this heading: male

competition and female choice. Both can be seen as components of a single mechanism: one being *intrasexual* (within one sex) and the other *intersexual* (between the sexes). This framework stresses competition between males for sexual access to females, engendering more or less pronounced sexual dimorphism and the development of armaments and ornaments in males.

Darwin proposed the concept of sexual selection to account for the differences in instincts and anatomy between male and female organisms. In principle, sexual selection applies to both males and females: it “depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction” [5]. But in fact, Darwin makes very clear that the special features of females (organs for the nourishment or protection of the young) are not his concern (they “do not here concern us”, vol. I, p. 254). Therefore, sexual selection can be described as a theoretical device mostly focusing on the evolution of males: the hypothesis that certain features of some males (not all) have been transmitted to their male offspring, as their bearers had gained an advantage over their rivals in accessing potential mates, fertilising eggs and leaving progeny. Darwin clearly states his concern: “Our difficulty in regard to sexual selection lies in understanding how it is that the males which conquer other males, or those which prove the most attractive to the females, leave a greater number of offspring to inherit their superiority than the beaten and less attractive males. Unless this result followed, the traits which gave to certain males an advantage over others could not be perfected and augmented through sexual selection” [5]. If sexual selection today designates differential reproduction due to mate competition [6], without any particular reference to males, it is nonetheless clear that females were mostly left out of Darwin’s picture, as was noted by the Unitarian minister Antoinette Blackwell as early as 1875 [7].

In the *Origin of Species* [8] (1859, pp. 87–90), the features attributed to sexual selection are of two sorts: weapons of the males, useful in fights with their rivals; ornaments of the males, such as beautiful feathers or songs, which may be preferred by females. Male–male competition explains such features as the antlers of deers, the horns of antelopes and of many beetles—any feature that supports males in their competition with other males of the same species, allowing winners access to the greatest number of females. But Darwin argued that traits such as the peacock’s tail, with no visible utility in intrasexual competition, must be selected by another type of factor. In Darwin’s words, “the peacock with his long train appears more like a dandy than a warrior, but he sometimes engages in fierce contests” [8] (1871, vol. II, p. 46). Darwin argued that females have a sense of beauty and are excited and charmed by the extravagant ornaments and displays of the best males. It seems that male–male competition was easily accepted by Darwin’s contemporaries, but that many (like A.R. Wallace) refused to accept the idea of female choice: How could a sense of beauty possibly be found among female deers and birds, let alone insects? The question had long been of concern to Darwin, who wrote in his notebooks: “How does hen determine which most beautiful cock, which best singer?” [9].

Darwin’s 1871 book *The Descent of Man and Selection in Relation to Sex* devotes two thirds of its content to sexual selection and goes more into detail.

Sexual selection can account for (1) sense organs, which may help in locating a potential partner; (2) locomotion organs, which may help in reaching the partner; and (3) prehensile organs, which can help in holding the partner while mating. In such cases, it is very difficult to differentiate between natural and sexual selection. In other cases, natural and sexual selection seem to contradict each other. Apparently, sexual selection primarily concerns extreme nonadaptive features such as the cumbersome train of the peacock. Understood from the peacock's perspective, sexual selection has to account for the evolution of extravagant "secondary sexual characters"—those "which are not directly connected with the act of reproduction" [8] (1871, vol. I, p. 253). Where utilitarian natural selection is ineffective, sexual selection will do the job. But it would be wrong to assume that sexual selection accounts for all sexual differences. Darwin clearly acknowledges that, in many instances, "it is scarcely possible to distinguish between the effects of natural and sexual selection" (vol. I, p. 257): for instance, prehensile organs may be helpful in grabbing food or in holding the sexual partner while mating.

Besides, the power of sexual selection is not limited to morphological traits: it also extends to habits and behaviours. In Darwin's text, the males are described as enterprising and not very discriminating, for instance male birds: "In all ordinary cases the male is so eager that he will accept any female, and does not, as far as we can judge, prefer one to the other" (vol. II, p. 121); or with insects and crustaceans, "the male is the more active member in the courtship of the sexes" (t. I, p. 272). On the other hand, females are depicted as shy, reticent or "coy": "The female, on the other hand, with the rarest exception, is less eager than the male. As the illustrious Hunter¹ long ago observed, she generally "requires to be courted"; she is coy, and may often be seen endeavouring for a long time to escape from the male" (vol. I, p. 273).

Darwin is willing to acknowledge the existence of exceptions to the above depictions²; still he thinks they encompass a general pattern, and that the exceptions are few. The cited sentences have been widely quoted and criticised as projecting Darwin's Victorian prejudices on the behaviours of animals.

As early as 1875, Antoinette Blackwell (1825–1921) noted that both male competition *and* female choice aim at explaining how *male* traits evolved by conferring a benefit to their bearer in situations of fight or seduction [7]. The Darwinian mechanisms aim to explain how evolution adds to the features of males, while female traits are considered to be basic. Neither intra- nor intersexual selections provide an explanation for female traits.

Besides, Darwin's distinction between coyness and eagerness had an important legacy regarding the ways in which sexual dimorphism was conceived of at the end of the nineteenth century. Two biologists based in Scotland, Patrick Geddes (1854–1932) and John A. Thomson (1861–1933), suggested that the features

¹ John Hunter (1728–1793), whose *Observations on certain parts of the animal oeconomy* (1786) were republished in 1840, with annotations by Richard Owen.

² Darwin did not think males were necessarily more "evolved" than females in the sense of possessing a "higher" degree of organisation. See, for instance, Darwin's analysis of rudimentary males in barnacles ([5], t. I, p. 255).

analysed by Darwin reveal what could be called the metaphysical essences of males and females: *maleness* and *femaleness* are interpreted as the manifestation of two kinds of energetic processes called *katabolic-disruptive* and *anabolic-accumulative*, respectively. Darwin had already stated that the “male is more liable to vary than the female”, and that “variations are more apt to occur in the male than in the female sex” (1871, t. I, p. 275, t. II, p. 128). Greater variational tendencies in males were used to equate males with a *progressive* element, a belief hastily taken up in Geddes and Thomson’s book *The Evolution of Sex* (1889) [10]. For them, many species clearly evince that, “*on an average*”, “the females incline to passivity, the males to activity”. This contrast may be less visible among “superior” organisms, but it seems to the authors that “even in the human species the contrast is recognised. Everyone will admit that strenuous spasmodic bursts of activity characterise men, especially in youth, and among the less civilised races; while patient continuance, with less violent expenditure of energy, is as generally associated with the work of women” [10] (1889, p. 18).

Geddes and Thomson even find this contrast among gametes, between the active male sperm and the seemingly awaiting female egg. They explain that males are stronger, more beautiful and more emotional than females, not because of sexual selection on their ancestors, but “simply because they are males—*i.e.* of more active physiological habit than their mates” [10] (1889, p. 24). Finally, they reinterpret the *eagerness* that Darwin attributed to males as a series of disruptive processes, while the alleged female *coyness* is understood as mere passivity: males live at a loss, while females live at a profit, the former being katabolic (consuming energy), the latter anabolic (accumulating energy). As a result, their book often figures prominently in the feminist collection of howlers, as the iconic example of male-centred prejudice. But Darwin’s view of eager males and coy females was still to thrive for many years.

6.2 Bateman’s Hardening of Sexual Dichotomies

In an influential paper published in *Heredity* in 1948, Angus J. Bateman endeavoured to search for “a fundamental cause of intramasculine³ selection, independent of mating system and probably inherent in the mechanics of sexual reproduction” [4] (p. 352).

Bateman wanted to understand why it seems “a general law” in nature “that the male is eager for any female, without discrimination, whereas the female chooses the male” (p. 352).

The conclusion of his genetic study of fruit flies, *Drosophila melanogaster*, was that males are “inherently subject to stronger selection than females”. This means

³“Intramasculine” designates a selection that occurs between males, as opposed to “female selection” or choice of mates on the part of the female.

that their contribution to the next generation is more variable than that of females (p. 367). All females have approximately the same success in mating, while the fertility and reproductive success of males is strongly dependent on their frequency of insemination. This difference of variance between the reproductive success of males and females entails what Bateman calls “undiscriminating eagerness in males and discriminating passivity in females” (p. 362).

In Bateman’s own words (1948, p. 365): “there is competition between male *gametes* for the fertilisation of the female *gametes*”. Because females produce many fewer gametes than males do, Bateman claimed that their fertility is much more limited than the fertility of the male. On the contrary, in the male, “fertility is seldom likely to be limited by sperm production”, and depends rather on their frequency of insemination (p. 364). Implicit in Bateman’s argument is the idea that sperm are less expensive to produce than eggs are.

Bateman’s paper was understood as evidence for the fact that “female multiple mating was unlikely to be very common as it was unlikely to enhance female fitness” [11].

Many critiques have been raised against Bateman’s conclusions. Above all, while being very forthcoming about polygamous tendencies in males, he did not actually monitor the courtship and promiscuous behaviour of fruit flies, nor did he directly measure the actual number of inseminations. Instead, he was using dominant marker genes and simply counting the carriers of the genes in the progeny. In other words, he only took into account inseminations that led to identifiable offspring [12, 13]. And even so, Bateman acknowledged that full identification was not always possible for about one fourth of the progeny (flies carrying two marker genes; 1948, p. 355).

Snyder and Gowaty also pointed out statistical mistakes and biased reporting in Bateman’s paper, concluding both that Bateman’s results are unreliable and that Bateman’s paper “retains its place as the single most important empirical observation in sexual selection” [14] (2007, p. 2457).

6.3 Expanding Bateman’s Paradigm

The problem with Darwin–Bateman’s opposition of male eagerness and female coyness is that it tends to associate a particular behaviour with each sex. The behaviour of individuals depends on the type of gametes they produce. Bateman’s paper strongly suggests that there are some genetic correlates to what Geddes and Thomson called “maleness” and “femaleness”. But it is not true that throughout nature, all males behave in the very same way, while all females behave in another—also unique—way.

Although selection might create a marked dimorphism in some species (the all-too-famous peacock), other cases exist in nature, cases revealing either little sexual dimorphism (magpies) or “sex-role reversal”, that is, species where the traditional Darwinian account of eager males and coy females is exactly the reverse: females

are gaudy and pugnacious, larger and more brightly coloured than males, pursuing them and aggressively competing for nesting territory, while males are drab and are in charge of incubation and care for the young. A genus of shore birds, the phalaropes (sea snipes), illustrates this.

Such cases can be taken into account by the concept of “parental investment”, which explains why certain individuals have more reproductive success than others. Robert L. Trivers (1972) defined parental investment as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence its reproductive success) at the cost of the parent’s ability to invest in other offspring” [15]. Elaborating among others on the work of Bateman on *Drosophila* and on William Hamilton’s study of the genetic evolution of social behaviour, Trivers’ 1972 paper perpetuates the idea that “the parental investment pattern that today governs the operation of sexual selection apparently resulted from an evolutionarily very early differentiation into relatively immobile sex cells (eggs) fertilized by mobile ones (spermatozoa)” [15]. Mobile sperm and immobile eggs are decisive elements in parental investment. The paper, no doubt, also bears heavily on the stereotypes of indiscriminate males and sexually restrained females: “the cost of the copulation itself is always trivial to the male, and in theory the male need not invest anything else in order to copulate” [15]. Any precopulatory contribution the male will make (like territory defence) seems usually “small compared to the cost of the eggs” [15]. This intrinsic difference in parental care investment between males and females is understood as leading to important consequences, making desertion and multiple mating (including extra-pair copulation) common features in the animal world. Trivers’ final words are the following: “Throughout, I emphasize that sexual selection favours different male and female reproductive strategies and that even when ostensibly cooperating in a joint task male and female interests are rarely identical” [15].

Trivers contends that the sex that invests the least in raising the young (*usually* but not *necessarily* the males) displays the greatest amount of variation in reproductive success, while the sex that invests the most becomes limiting for the other sex. Although Trivers has been abundantly cited in support of the “fact” of male aggressiveness and female passivity, the concept of “parental investment” enables one to understand that it is not the biological sex that determines the intensity of sexual selection and, consequently, the extent or modalities of sexual dimorphism. If there are circumstances in which males invest more and females become sexually competitive, they clearly challenge the focus on gametes as the sole or main estimate of parental investment.

6.4 Anisogamy and the Feminist Challenge to Sexual Selection

Trivers’ concept of parental investment makes clear that female choosiness and male promiscuity are conceived of as based on “anisogamy”, a word coming from the Greek (*an*, not; *iso*, the same), which means that the gametes of the males and

the gametes of the females are not the same and especially not of the same size or cost. Thus understood, the difference between males and females means only one thing: the two-sex divide and the division between “coyness” and “eagerness” are supposed to be the mere behavioural equivalent of those gametic “facts”: females with costly eggs are depicted as careful investors, while males with cheap sperm seem readier to mate. In fact, these assumptions are flawed in many different ways.

First, it should be noted that anisogamy is not a necessity in nature. In some species, sexual reproduction occurs in cases of isogamy (with gametes of the same size). More importantly, most of the literature on anisogamy has focused on the idea that sperm are cheap. But is this so? In the fruit fly *Drosophila bifurca*, the sperm is twenty times longer than the size of the male who made it. It is so expensive that males conserve their sperm and it leads to a one-to-one gamete ratio. Such sperm don't come “cheap”, and males take twice as long to mature as females. As to anisogamic species, it is a fallacy to compare the cost of one egg with the cost of one sperm, because an ejaculate consists of millions of sperm and other glandular secretions. In many species (cockroaches, butterflies), male sperm is accompanied by various nutrients in addition to the genetic material. The possibility of sperm depletion has to be taken into account: sperm undeniably has a cost. Far from being a limitless resource, it is subject to caution allocation, a fact that entails the existence of male mate choice, contrary to narratives of indiscriminate male behaviours. The traditional account of anisogamy should be taken with caution, even though gamete production undeniably has a cost. Female/feminist biologists like primatologist Sarah B. Hrdy have both criticised the idea that males produce “cheap” gametes and the “American supermarket mentality” built into the anisogamy argument that tends to forget that resources can be scarce [16]: gamete production has a cost, which should not be overlooked. The real issue is to determine what cost assessment must take into account.

The traditional “anisogamy” account is also flawed in that “coyness” is not a fact. In the 1970s, several women primatologists were focused on what female animals were actually doing [16, 17]: they were trying to remind their colleagues that females are also actors and described the modes of competition or collaboration among them. Hrdy's study on langurs shows how females, far from being “coy”, actively seek coitus, a behaviour that can be used to sow doubt as to the identity of the father and so have the effect of lowering the rate of infanticide [17]. The literature on polyandry as a common female mating strategy has expanded during recent decades. It is now well known that females in many bird species solicit from other males and actively engage in extra-pair copulations (EPCs)—contrary to the common assumption that EPCs were systematically initiated by male intruders.

Moreover, feminist biologists have made clear that Darwin's two-sex model of sexual selection was clearly biased in favour of the male sex, leading to what Hrdy called, after Antoinette Blackwell, “the woman that never evolved” [16]. Whereas the Darwinian paradigm of sexual selection wrongly concentrated on two factors (male–male competition and female choice), evolutionary biologist Patricia Gowaty has extended the list of selective forces and factors of success in reproduction: female competition for resources; female choice of partners; male

behaviours opposing female choice, like sexual coercion; female resistance to this coercive control; male competition for coercive access to females; competition between males and females for control of resources essential to reproduction; and male competition for resources [18]. Others have emphasised the importance of non-reproductive behaviours in nature, particularly sexual dynamics other than male-female [2, 19].

In spite of those critics, the anisogamy thesis is supported by the fact that gametes often come only in two forms, small and large: gamete size is not a continuum. Organisms with three or more gamete sizes are exceedingly rare—for instance, the green ciliate *Chlamydomonas euchlora* [3]. As we have seen earlier, this feature is crucial to the standard biological definitions of a “male” (an individual making small gametes) and a “female” (one making large gametes), the smaller of the two gametes being called a *sperm*, the other the *egg*. Gamete size plays a key role in defining both male and female “strategies” (the word “strategy” referring here to “a blind unconscious behaviour program”—Maynard Smith quoted by Dawkins 2006 [20]). According to this genetic definition of sex, there is today a general consensus that, at least in vertebrates, species with a sexual reproduction are divided into two and only two sexes. But there may be, within one sex in a single species, several “morphs” or aspects: for instance, there may be two types of females, those reproducing sexually and those reproducing asexually (“parthenogenetically”); or, in some species of fish, birds or mammals, two types of males, one generally identified as the male sex and the other which is more juvenile or “feminised” in his aspect. The different “morphs” in one sex can be called different “genders”.⁴ The males who do not match the dominant type are generally neglected (hastily identified as females) or called “sneakers”. If sperm-producing individuals come in different morphs, with different behaviours, then doesn’t it become impossible to define something like a “typical male behaviour”? Another recent challenge to sexual selection theory deals with the preferences of females: should all females go for the more “masculine” males, and are the others necessarily “sneakers”? Recent studies show that females may prefer the “feminised” males, and that those males may play an important role in assorting pairs [3, 22].

The anisogamy thesis of the difference of the sexes expands on the old metaphysical dichotomy activity/passivity and considers female processes as less worthy than their male counterparts. This tendency towards androcentrism (i.e. male-centredness) might be called “inadvertent machismo” [23]: it pervades not only the evolutionary science of animal behaviour but also conceptualisations of the cell, of the bacterial world or textbooks on reproduction, and it has been strongly criticised in feminist critiques [24–26].

⁴I follow here Joan Roughgarden’s suggestion (2004): “sex” refers to the two individuals producing the two different types of gametes (eggs/sperm, conventionally defining what is a male and what is a female), while “gender” refers to the different morphs in one sex. Matt Ridley [21] makes a different use of the terms: “sex” refers to sexual (vs asexual) reproduction, while “gender” refers to the distinction between “males” and “females”, two terms that Ridley understands as defining two different “natures”.

6.5 Perspectives: The Search for Gender-Neutral Models

Dissatisfaction with Bateman's paradigm has led several evolutionary biologists to emphasise that variances in lifetime reproductive success between males and females are not necessarily linked to mate choice or male–male competition but that they could be explained by chance effects and both sexes mating randomly.

Important papers by William Sutherland (1985) [27] in the UK, Hubbell and Johnson (1987) [28] in the USA and Michel Veuille in France [29, 30] (1982, 1986) have also suggested that the variance in male mating success presented in Bateman's paper was the value expected under a Poisson law, that is, that corresponding to the variation in mating success resulting from random encounters with unmated females. This idea was further developed by Gowaty and Hubbell [11, 31]: they provided new models to quantify nongenetic factors, such as chance and time, to account for variations in lifetime reproductive success. Their model, called SPT (switch point theorem), considers how “variation in encounters, latencies, survival, and their more complex proxies (relative reproductive rate, the operational sex ratio, and density) favours shifts in mean behaviour of the sexes and as a result more nuanced reports of ecologically induced variation in sex-typical behaviour” [31]. Those new tools allow testing of sex role flexibility in both sexes, instead of assuming the Darwin–Bateman two-sex hypothesis of two defined strategies. The emphasis on time in mating processes suggests a focus on environmental (i.e. nongenetic) constraints of variation and on chance effects on the number of mates.

Such aleatory factors have already been taken into account by classic papers in behavioural ecology (such as Trivers [15]), but their importance was then overshadowed by an extreme gametocentrism (the anisogamy thesis), with essentialist overtones: instead of studying populational or individual behaviours, biologists were haunted by the search for “maleness” and “femaleness”. Differences in parental investment between males and females and the existence of anisogamy do not imply that males are necessarily indiscriminate in their matings or that sperm come cheap. Richard Dawkins stated, in a very Geddes-and-Thomson fashion, that “the word *excess* has no meaning for a male” [10]: Does this sentence refer to the profligacy of males, and how does it cover the case of males from several species dying from exhaustion after mating? Two-sex models, in the tradition of the Darwin–Bateman paradigm (coyness vs eagerness), are an exact replica of the metaphysical dichotomy between passivity and activity. Besides, the existence of two sexes, or two types of gametes, does not entail the existence of two (and only two) types of behaviours: one for males, one for females. As already suggested, there might be several “genders” or mating types in one sex.

Given the numerous challenges to the Darwin–Bateman paradigm, Joan Roughgarden and her lab proposed replacing the competitive framework of sexual selection with cooperative game theory models [3]. In species with sexual reproduction, evolutionary success is not only about mating: in order to complete the task

of reproduction, individuals have to breed and raise their young until they are sexually mature.⁵

Biologists are facing the challenge of devising new models that avoid gender stereotypes or essentialist assumptions about “males” and “females” and the way they should behave. When tested against the prevailing traditional predictions, these new models may better account for the variation we keep on discovering in nature.

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⁵The question then arises as to whether such attempts broaden the theoretical framework of behavioural ecology, renew it completely, or rather but underscore certain possibilities already implicitly present within the existing sexual selection framework.

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