

REVIEW

The 150th anniversary of *The Descent of Man*: Darwin and the impact of sex-role reversal on sexual selection research

KAROLINE FRITZSCHE¹, JONATHAN M. HENSHAW¹, BERNADETTE D. JOHNSON² and ADAM G. JONES^{2,*}

¹*Institute of Biology I, University of Freiburg, Hauptstraße 1, D-79104 Freiburg, Germany*

²*Department of Biological Sciences, University of Idaho, Moscow, ID 83844, USA*

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The year 2021 marks the 150th anniversary of the publication of Charles Darwin's extraordinary book *The Descent of Man and Selection in Relation to Sex*. Here, we review the history and impact of a single profound insight from *The Descent of Man*: that, in some few species, females rather than males compete for access to mates. In other words, these species are 'sex-role reversed' with respect to mating competition and sexual selection compared to the majority of species in which sexual selection acts most strongly on males. Over the subsequent 150 years, sex-role-reversed species have motivated multiple key conceptual breakthroughs in sexual selection. The surprising mating dynamics of such species challenged scientists' preconceptions, forcing them to examine implicit assumptions and stereotypes. This wider worldview has led to a richer and more nuanced understanding of animal mating systems and, in particular, to a proper appreciation for the fundamental role that females play in shaping these systems. Sex-role-reversed species have considerable untapped potential and will continue to contribute to sexual selection research in the decades to come.

ADDITIONAL KEYWORDS: Bateman gradient – evolution – male pregnancy – mating systems – operational sex ratio – opportunity for sexual selection – parental investment – potential reproductive rates – sex roles.

INTRODUCTION

'So that with this emu we have a complete reversal not only of the parental and incubating instincts, but of the usual moral qualities of the two sexes; the females being savage, quarrelsome and noisy, the males gentle and good'.

(Charles Darwin, 1871: p. 205).

Darwin's engagement with species displaying atypical sex roles illustrates the importance of natural history in the study of evolutionary biology, for his careful consideration of the habits of particular species clearly shaped his views on sexual selection. His most complete example of unusual sex roles came from the barred buttonquail, *Turnix suscitator* (known

to Darwin as *Turnix taigoor*). In this species, the female is larger and more colourful than the male. Furthermore, 'the female appears to be vociferous, and is certainly much more pugnacious than the male; so that the females and not the males are often kept by the natives for fighting, like game-cocks' according to Darwin. He goes on to note that the females leave the males to care for the offspring. Few modern studies have investigated issues related to sexual selection in this species; however, their findings generally support Darwin's account (Muck & Goymann, 2011, 2019; Voigt, 2016). Darwin additionally discusses a number of other bird species in which the females are more brightly coloured or more aggressive than the males. His examples include painted snipes, two phalaropes, the Eurasian dotterel, the Southern cassowary, the emu and a few other species for which he had only sketchy observations. He was also aware of male

*Corresponding author. E-mail: adamjones@uidaho.edu

pregnancy in pipefishes; however, misleading reports of the males being the more colourful sex excluded them from his consideration as species with stronger sexual selection in females.

The unusualness of such species was clear to Darwin, who contrasted them with the more typical scenario where mating competition is stronger among males than females. He wrote, ‘It is certain that with almost all animals there is a struggle between the males for the possession of the female. This fact is so notorious that it would be superfluous to give instances’. Darwin did not use the term ‘sex-role reversal’, however, which was coined in the modern sexual selection literature. This term is deservedly controversial (Ah-King & Ahnesjö, 2013). Nonetheless, the term has served as an organizing banner for a broad party of researchers studying ‘unusual’ sex roles and their implications for sexual selection theory. In the sexual selection literature, ‘sex-role reversal’ most often, and in our view most aptly, describes the situation in which females, rather than males, are the primary competitors for access to mating opportunities (Vincent *et al.*, 1992; Eens & Pinxten, 2000; Hare & Simmons, 2020). Sexual selection accordingly acts more strongly on females than on males, often selecting for ornaments, armaments or other traits that give females an advantage in mating competition (reviewed in Hare & Simmons, 2020). Of course, sex differences in mating competition also coevolve with other important traits, most notably with parental care (Trivers, 1972; Fromhage & Jennions, 2016; Janicke *et al.*, 2016; Royle *et al.*, 2016; Henshaw *et al.*, 2019).

The consideration of sex-role-reversed species led Darwin to insights that would have been impossible without reference to such taxa. First, perhaps the most profound conclusion was that sexual selection need not act only on males. In other words, competition for mates is not an inseparable component of maleness. Sometimes, the female can be the competitor for mates, and under such circumstances, the female may evolve to be the sex that is the most ‘pugnacious’, ‘pugilistic’ or ‘courageous’ in competition for mates. These choices of adjectives are an unfortunate by-product of 19th century society, and we now know that the choosing sex often plays an active and important role in the mating process, a point we will revisit later.

Second, from Darwin’s perspective, the idea that sexual selection sometimes acts primarily on females called for an explanation. Why do species evolve to be sex-role reversed and, more generally, what factors determine the intensity of sexual selection? Although never providing a wholly satisfactory explanation, Darwin’s attempt to explain sex-role reversal set the stage for more successful work nearly a century later. In particular, he explicitly invoked an argument based on the sex ratio: ‘if we might assume that the females have

become much more numerous than the males—and in the case of one Indian Turnix the females are said to be “much more commonly met with than the males”—then it is not improbable that the females would have been led to court the males, instead of being courted by them’. This argument suggests that the economics of mate availability might have something to do with sexual selection, an idea that was later picked up by Emlen and Oring (1977) and that underlies much of modern sexual selection theory. Darwin even presaged the role of parental and other reproductive investment in determining the strength of sexual selection, noting that ‘the female has to expend much organic matter in the formation of her ova, whereas the male expends much force in fierce contests with his rivals.... On the whole the expenditure of matter and force by the two sexes is probably nearly equal, though effected in very different ways and at different rates’. This idea was later given a firmer foundation by Trivers (1972) and Williams (1975) (see below). Darwin also proposed a number of explanations that are less compelling, at least from an evolutionary perspective. For example, he argued that males of sex-role-reversed species ‘have lost some of their ardour which is usual to their sex, so that they no longer search eagerly for the females’. Later work honed in on proximate explanations for this apparent ‘loss of ardour’ and other atypical sex-specific behaviours, and this topic remains a very active area of research (Rissman & Wingfield, 1984; Fivizzani *et al.*, 1986; Gratto-Trevor *et al.*, 1990; Eens & Pinxten, 2000; Goymann & Wingfield, 2004; Muck & Goymann, 2011; Voigt, 2016; Lipshutz & Rosvall, 2020).

Third, Darwin’s consideration of sex-role reversal was important because it naturally suggests a continuum of mating competition, with strong sexual selection on males and females at each end point. At intermediate points on this continuum, sexual selection could act on both sexes or perhaps neither, possibilities that Darwin did consider. For instance, he believed that the larger size and greater physical strength in human males arose as a consequence of direct contests among males for mating opportunities; however, he also believed that human females were subject to sexual selection, mainly through the mechanism of male choice (Darwin, 1871). The idea that sexual selection could act on either or both sexes was thus present in the earliest manifestation of Darwin’s theory. It seems plausible that this appreciation for sexual selection on both sexes was due partly to Darwin’s awareness of sex-role reversal in the natural world.

In the decades that have passed since the publication of *The Descent of Man*, many additional examples of sex-role reversal have been discovered and studied (Fig. 1), and these discoveries have profoundly shaped the field of sexual selection. We set our rudder by introducing some of the most influential examples of

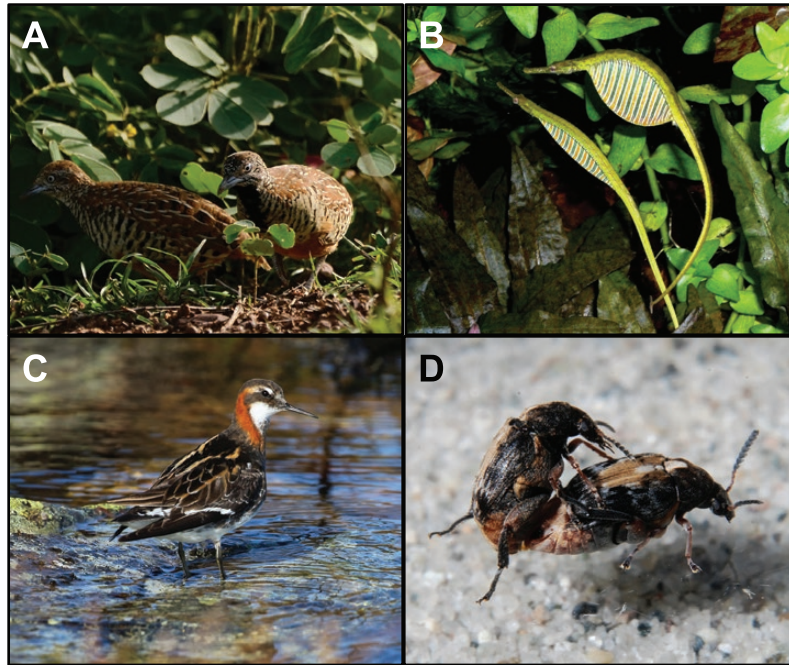


Figure 1. A sample of sex-role-reversed taxa that have shaped the direction of sexual selection research over the past 150 years by serving as the ‘exceptions that prove the rule’. A, the barred buttonquail provided Charles Darwin with fodder for thought experiments as he contemplated the factors that affected the strength of sexual selection in nature. The female (right) is larger and more ornamented than the male. B, male pregnancy in pipefishes and seahorses has provided numerous opportunities for thought experiments and actual experiments from the 1960s to the present. Two females of the pipefish *Microphis deocata* are shown here displaying the colorful flaps that they unfurl during courtship. C, the red-necked phalarope played a prominent role in the thinking of Stephen Emlen and Lewis Oring as they generated ideas that revolutionized the relationship between ecology and sexual selection. A female is shown here—males are smaller and duller. D, the honeylocust beetle is a sex-role-reversed insect amenable to laboratory study. Such experimentally tractable taxa may shape the future of laboratory-based research on sex-role reversal. Photo credits: (A) P Jeganathan ([https://commons.wikimedia.org/wiki/File:Barred_buttonquail_or_Common_bustard-quail_\(Turnix_suscitator\)_from_Andhra_JEG7344.jpg](https://commons.wikimedia.org/wiki/File:Barred_buttonquail_or_Common_bustard-quail_(Turnix_suscitator)_from_Andhra_JEG7344.jpg)), CC BY-SA 4.0. (B) Günther Halbauer / UNTER WASSER (with permission) (C) Ingeborg van Leeuwen (https://www.flickr.com/photos/ivl_wildlife_photography/50033623826), CC BY-NC-ND 2.0. (D) Janos Bodor (with permission).

sex-role-reversed species (Box 1). Then, we discuss the development of sexual selection theory, from a sex-role-reversed perspective, and finally we conclude with some comments about how sex-role-reversed organisms might contribute to the future of the study of sexual selection.

SEX-ROLE REVERSAL AND ITS CONTRIBUTION TO SEXUAL SELECTION RESEARCH

A first acquaintance with sex-role reversal is best obtained by taking a tour of species that exhibit unusual sex roles (Fig. 1). Such species have been described in many different taxonomic groups, including birds, fishes and insects; however, they are conspicuously absent from some other groups, like mammals and reptiles (Box 1). The overall rarity of sex-role reversal belies its impact on the development of sexual selection theory. A mere

awareness of sex-role-reversed species stimulated many of the thought experiments that helped forge our modern understanding of sexual selection. Beginning about a century after Darwin first wrote about sex-role-reversed birds, the field experienced a series of conceptual breakthroughs, with sex-role-reversed species present at each important step. An ‘exception proves the rule’ attitude permeates the study of sex-role reversal; however, such ‘rules’ might never have come to be without the thought experiments inspired by role-reversed taxa. Here, we discuss how sex-role reversal has shepherded the development of modern sexual selection theory.

THE REBIRTH OF SEXUAL SELECTION: PARENTAL INVESTMENT THEORY

‘If there were no such animals as seahorses or tinamous, the explanation offered would be

Box 1: Which taxa are sex-role reversed? An introduction to influential species

The early development of sexual selection theory owes much to sex-role-reversed birds—Darwin (1871), Williams (1966, 1975), Trivers (1972) and Emlen and Oring (1977) all relied on role-reversed waders to inspire and support their arguments. Painted snipes (*Rostratula* sp.), spotted sandpipers (*Actitis macularius*), phalaropes (*Phalaropus lobatus*, *Phalaropus tricolor*), the Northern jacana (*Jacana spinosa*) and the Eurasian dotterel (*Charadrius morinellus*) are mentioned for their intensive male brood care and competition among females for access to mates. Males provide most of the parental care in these species, incubating the eggs and brooding chicks, which frees up the females to seek additional mating opportunities. Successful females can mate with several males, resulting in a shortage of males and competition among females for mates (Oring & Lank, 1986; Andersson, 2005). As a consequence of this competition, females have evolved to be larger, more aggressive or more colourful than males (Oring *et al.*, 1991; Owens & Thompson, 1994; Delehanty *et al.*, 1998; Emlen & Wrege, 2004b; Blizard & Pruett-Jones, 2017). More recently, sex-role reversal has been documented in many other bird species, including the black coucal (Goymann *et al.*, 2004, 2016; Safari *et al.*, 2019) and various ground feeders and shorebirds in the order Charadriiformes [reviewed in Eens & Pinxten (2000); Hare & Simmons (2020)]. Sex-role reversal in birds is universally associated with substantial male parental care, and in most species a single female can leave eggs in the care of more than one partner.

Sex-role-reversed fishes from the family Syngnathidae, which includes pipefishes, seahorses and seadragons, are another well-studied group (Berglund & Rosenqvist, 2003; Wilson *et al.*, 2003). This family was known already to Williams and Trivers and helped them to solidify their theory on mating system evolution (Williams, 1966, 1975; Trivers, 1972). From a sexual selection perspective, syngnathid fishes are most noteworthy for their pattern of parental care, in which females transfer eggs to the male, who provides all parental care. In some species, the male possesses a pouch that completely envelops the eggs, a mode of parental care that is accurately described as ‘male pregnancy’ (Paczolt & Jones, 2010). The male’s investment in offspring ends at parturition, whereas the female’s investment ends considerably earlier, at mating, potentially freeing her up to seek additional mating opportunities. In some syngnathid species, females compete intensely for access to additional mates and have evolved elaborate ornaments and behaviours associated with mating competition (e.g. Rosenqvist, 1990; Rosenqvist & Berglund, 2011; Flanagan *et al.*, 2014).

A number of fish species outside of the syngnathids also exhibit sex-role reversal. An intriguing example is the two-spotted goby (*Gobiusculus flavescens*), in which males compete for mates early in the season, whereas females compete later in the season. This change in the direction of sexual selection results from a shift in the ratio of sexually available males and females as the season progresses (Forsgren *et al.*, 2004; Wacker *et al.*, 2013; Amundsen, 2018). Some close relatives of the two-spotted goby, such as the blue-banded goby (Pradhan *et al.*, 2015) and the peacock blenny (Saraiva *et al.*, 2009, 2012), along with some phylogenetically distant fishes [e.g. the black-chinned tilapia (Balshine-Earn & McAndrew, 1995)], are also sex-role reversed. Convincing examples of sex-role reversal in fishes, however, are less common than expected, most likely as a result of a severe lack of behavioural data for most fish species (Vincent *et al.*, 1992).

Most other documented cases of sex-role reversal come from the insects, including honeylocust beetles (Takakura, 1999, 2006; Fritzsche *et al.*, 2016), katydids (Gwynne, 1981, 1993; Simmons, 1992), giant water bugs (Smith, 1979; Ichikawa, 1989; Gilg & Kruse, 2003) and dance-flies (Svensson & Petersson, 1987; Funk & Tallamy, 2000; Murray *et al.*, 2018). In many of these species, the evolution of female mating competition is driven not by male parental care, but rather by substantial nuptial gifts (e.g. prey items or spermatophores) that males provide during courtship or mating. In vertebrates, very little sex-role reversal has been documented outside of birds and fishes. Although male care is fairly common in amphibians, only a few species, including midwife toads (Verrell & Brown, 1993; Bush & Bell, 1997) and the smooth guardian frog (*Limnodynastes palauensis*) of Borneo (Byrne & Keogh, 2009; Byrne & Roberts, 2012; Goyes Vallejos *et al.*, 2017, 2018), appear to be strong candidates for sex-role reversal. No mammals or reptiles have been documented as sex-role reversed.

Regardless of the taxonomic group, sex-role reversal is rare. The intense research interest in certain birds and fishes can foster a misleading impression that sex-role reversal is fairly commonplace; however, even a generous estimate places less than one in a hundred species in this category. Across taxonomic groups, the general pattern is that a small handful of phylogenetically dispersed species have idiosyncratically evolved sex roles that differ substantially from their taxonomic norm. Across taxa, strong mating competition among females is closely linked to substantial male investment in either offspring or mates. Accordingly, female-biased mating competition is more common in taxa in which ecological and life-history conditions favour the evolution of paternal care. Nonetheless, why sex-role reversal is so rare and why some taxonomic groups are more prone to its evolution than others remain controversial questions (Henshaw *et al.*, 2019).

compatible with the evidence but not forcefully supported. It is the exceptions to the rule of masculine males and feminine females that prove the theory that explains both rule and exception’.

(George Williams, 1975: p. 134).

The theory of sexual selection remained dormant for nearly a hundred years. Other than a few studies, including a short but significant treatment by Ronald Fisher (1930) and a key study by Angus John Bateman (1948), which we will discuss later, almost no meaningful work was completed on this topic until the 1970s. Although Darwin, Fisher and Bateman did suggest some reasons that sexual selection more often affects males than females, the first profound insight and convincing explanation was laid down in Robert Trivers’ classic 1972 chapter on parental investment. This contribution was preceded by Williams’ 1966 book, *Adaptation and Natural Selection*, where he touches upon parental investment as a driver of the strength of sexual selection but does not fully develop the theory behind it:

‘Even without such special female functions as pregnancy and lactation, it is almost always true that females contribute the greater amount of material and food energy to the next generation. A female can readily increase her reproductive effort merely by increasing the mass of gametes to the point at which further gain would not be worth the sacrifice. For males, especially in species with internal fertilization with its great economy of sperm, the problem is not so simple. A male can easily produce sperm in excess of what it would take to fertilize all the females that could conceivably be available. The reproductive effort involved in male gametogenesis would ordinarily be slight. Most of his reproductive effort can be devoted to the problem of increasing the number of females available for insemination. Hence the development of the masculine emphasis on courtship and territoriality or other forms of conflict with competing males.

An important test of this explanation is whether the expected exceptions to this difference in male and female approaches to reproduction can be demonstrated. In some species the males contribute more materials in providing for the next generation or undergo greater risks in their essential roles. The best example I know is in the pipefish-seahorse family, the Syngnathidae. In this group the females, in copulation, are not inseminated by the males. Instead, they transfer their eggs to a brood pouch in the male. There the young develop to an advanced stage with the help of a placental connection with the male blood stream. Under the circumstances, we might expect

that it would be the female that would show the traditional masculine aggressiveness in courtship and general promiscuity, and the male that would show caution and discrimination. This is known to be true in some species, and it is not known to be untrue in any...’.

Williams (1966, 1975) thus understood that the relative parental investment of males and females is a key factor shaping sex differences in mating competition. It is Trivers (1972), however, who deserves credit for the first evolutionarily relevant definition of parental investment and for highlighting its critical role in the process of sexual selection. Trivers defined parental investment as ‘any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring’. Trivers’ crucial insight was that the sex investing more in parental care should be choosy, and individuals of the sex investing less should compete among themselves for access to mating opportunities (Trivers, 1972):

‘Where male parental investment per offspring is comparable to female investment one would expect male and female reproductive success to vary in similar ways and for female choice to be no more discriminating than male choice. Where male parental investment strongly exceeds that of the female one would expect females to compete among themselves for males and males to be selective about whom they select as a mate’.

Larger disparities in parental investment between the sexes should translate into stronger sexual selection on the competing sex. Trivers pointed out that sex-role-reversed taxa provide a key test of parental investment theory: ‘To test the importance of relative parental investment in controlling sexual selection one should search for species showing greater male than female parental investment (see Williams, 1966: 185–186)’. Trivers (1972) highlighted phalaropes, syngnathid fishes and a species of frog as examples of sex-role-reversed species supporting his argument regarding parental investment:

‘Likewise high male parental investment in pipefish and seahorses (syngnathidae) correlates with female courtship and coloration (Fiedler 1954) and female reproductive success might be limited by male parental investment’.

Trivers thus gave researchers a potentially testable theory with a key variable—parental investment—that empiricists could endeavour to measure. In the process, he also rediscovered Bateman’s (1948) fly experiment, which inspired later efforts to integrate

sexual selection into quantitative selection theory (see below). In practice, parental investment has proven difficult to quantify precisely; however, it remains a key heuristic underpinning of sexual selection theory and certainly plays an important role in determining the strength and direction of sexual selection. These latter conclusions are forcefully supported by the observation that every sex-role-reversed species is characterized by substantial male investment in either offspring or their mates. For instance, post-zygotic parental care is exclusively provided by the male in sex-role-reversed shorebirds (Oring & Lank, 1986; Colwell & Oring, 1988; Delehanty *et al.*, 1998; Emlen & Wrege, 2004a), coucals (Andersson, 1995; Goymann *et al.*, 2016), pipefish and other fish species (Breder & Rosen, 1966; Balshine-Earn & McAndrew, 1995; Swenson, 1997; Berglund & Rosenqvist, 2003; Saraiva *et al.*, 2012; Pradhan *et al.*, 2015) and giant water bugs (Smith, 1979; Ichikawa, 1989; Gilg & Kruse, 2003). In other sex-role-reversed taxa, males provide their mates with substantial nuptial gifts in the form of prey items [e.g. dance flies (Svensson & Petersson, 1987; Funk & Tallamy, 2000; Murray *et al.*, 2018)] or spermatophores [e.g. honeylocust beetles (Takakura, 1999, 2006; Fritzsche *et al.*, 2016), katydids (Gwynne, 1981, 1993; Simmons, 1992)].

The empirical association between sex differences in mating competition and parental investment is beyond doubt. Nonetheless, the theoretical relationships between these two variables have been the source of considerable and continued controversy. Importantly, it is insufficient to consider how fixed patterns of parental investment shape mating competition, as these two variables are expected to influence each other mutually and thus to coevolve (McNamara & Wolf, 2015; Fromhage & Jennions, 2016; Lehtonen *et al.*, 2016; Henshaw *et al.*, 2019). Trivers (1972) provided two main arguments for the maintenance of female-biased care and male-biased mating competition that is observed in most taxa. First, he claimed that when the mother has already invested more resources in a brood than the father, then a cessation of parental investment is more detrimental to maternal than paternal fitness due to the female's 'sunk cost'. This argument was later criticized as a 'Concorde fallacy' and is no longer taken seriously (Dawkins & Carlisle, 1976; Grafen & Sibly, 1978; Kokko & Jennions, 2008).

Second, Trivers argued that for the sex under stronger sexual selection, any increase in parental investment might trade off against traits involved in mating competition, potentially drastically reducing an individual's mating success. This could generate a positive feedback that maintains current sex roles. This argument has held up to theoretical scrutiny, although it is important to note that the expected evolutionary outcomes can depend on the details of

trade-offs in non-trivial ways (Fromhage & Jennions, 2016). In contrast to these expectations, Kokko and Jennions (2008) claimed that individuals of the less-caring sex have an incentive to increase care rather than re-enter the mating pool, because they are less likely to find a new mate than are individuals of the more-caring sex (see discussion of the operational sex ratio below). Although initially attractive, this argument is incorrect as it rests on a conceptual error. If the adult sex ratio is even, then the expected fitness of an average male entering the mating pool equals that of an average female (Fromhage & Jennions, 2016). Importantly, the evolution of sex-role reversal implies that positive feedback loops acting on sex roles can be broken, but we are only just beginning to understand the evolutionary mechanisms (Henshaw *et al.*, 2019; Iyer *et al.*, 2020). Interestingly, recent work on birds has demonstrated that caring males may not be quite so unavailable for matings as was once assumed, undermining the assumption of a strong trade-off between paternal care and mating activity (Schwagmeyer *et al.*, 2016; Safari *et al.*, 2019).

THE OPERATIONAL SEX RATIO AND THE ENVIRONMENTAL POTENTIAL FOR POLYGAMY

Another watershed moment in the study of sexual selection was Stephen Emlen and Lewis Oring's 1977 paper on the evolution of mating systems. Emlen and Oring (1977) elaborated the idea that mating system evolution is determined by (i) the 'environmental potential for polygamy', which is the degree to which competitors can monopolize access to multiple mates; and (ii) the 'operational sex ratio' (OSR), defined as the ratio of fertilizable females to sexually active males at any given time in the population. Emlen and Oring cemented their arguments by discussing sex-role-reversed bird species such as the spotted sandpiper (*Actitis macularia*), the Northern jacana (*Jacana spinosa*) and the red-necked phalarope (*Phalaropus lobatus*):

'Since an individual male is not able to maintain sexual activity indefinitely during incubation, males sitting on eggs normally must be considered sexually "unavailable". To the degree that females can produce more clutches than can be serviced by males (caused either by high production rates of females or low failure rates of existing clutches), the operational sex ratio will become skewed with a shortage of males. These conditions lead to increased intrasexual competition among females for access to available males. The degree to which polyandry will develop then depends on

the intensity of female sexual selection and the environmental potential for monopolization of mates...?.

This example highlights the connections to Trivers' prior theory, in that the OSR is influenced by the relative parental investment of each sex. Emlen and Oring's work led to two major advances in thinking about sexual selection. The first was an understanding that environmental conditions play a critical role in the mating dynamics of populations. The second was the idea that mating competition can be viewed in terms of the economics of mate availability. If more individuals of one sex than the other are available to mate, then the rarer sex should choose and the more common sex should compete. This idea dated back to Darwin; however, Emlen and Oring explicitly defined the sex ratio in terms of individuals ready to mate. Moreover, they emphasized that mating systems do not just come in two varieties, but rather are highly variable and follow a continuum: 'We are now coming to realize that variability in social organizations, including mating systems, is widespread'. Emlen and Oring's insights inspired researchers to measure the OSR and test its role in sexual selection. A prime illustration comes from the two-spotted goby. In this species, males compete for females early in the breeding season; however, the OSR becomes female-biased as the season progresses, leading females to actively compete for males (Forsgren *et al.*, 2004; Wacker *et al.*, 2013; Amundsen, 2018). Similarly, in the katydid *Kawanaphila*, Simmons (1992) could induce reversals in courtship roles experimentally via dietary limitation. At low levels of food availability, female gametogenesis was resource limited and so females competed for the nuptial gifts provided by males. In contrast, when food availability was high, females did not compete for mates. By now a large body of research, both empirical and theoretical, supports the entanglement of parental investment, sexual selection and the OSR (Colwell & Oring, 1988; Gwynne, 1990; Kvarnemo & Ahnesjö, 1996; Weir *et al.*, 2011; Moura & Peixoto, 2013; Fritzsche *et al.*, 2016; Fromhage & Jennions, 2016; Janicke *et al.*, 2016; Eberhart-Phillips *et al.*, 2018; Janicke & Morrow, 2018; Henshaw *et al.*, 2019).

THE POTENTIAL REPRODUCTIVE RATES OF THE SEXES

'...in species where males are responsible for all parental care while females pay the costs of egg production...the direction of mating competition differs between species. In some, females compete intensely for mates, males are choosy in selecting

partners and females are brighter than males. In others, males compete intensely for females, females are choosy in selecting partners, and males are brighter than females. An explanation for these differences could be that only in some of these species does the involvement of males in parental care depress their potential reproductive rate below that of females'.

(Tim Clutton-Brock & Amanda Vincent, 1991).

The operational sex ratio turned out to be difficult to measure in most systems (Székely *et al.*, 2014; Carmona-Isunza *et al.*, 2017), resulting in a search for other mating system parameters that are easier to quantify. The potential reproductive rate (PRR) is one such measure, and its development was facilitated by a consideration of sex-role-reversed taxa. Clutton-Brock & Vincent (1991) defined the potential reproductive rate as the 'maximum number of independent offspring that parents can produce per unit time'. They illustrated this concept by using the example of the 'polyandrous spotted sandpiper *Actitis macularia*, where females compete intensely for mating partners, males do not raise more than one clutch of four eggs during the breeding season, whereas females can lay an egg a day and lay clutches for up to four different males in the course of the season'.

Clutton-Brock and Vincent argued that the relative PRR of the sexes is strongly linked to the strength and direction of sexual selection (i.e. whether it acts more strongly on males or females). Their analysis showed that in sex-role-reversed taxa, PRR was nearly always higher in females, whereas male PRR was higher in species with strong sexual selection in males. They concluded that sex differences in PRR can predict the direction of mating competition and thus the direction of sexual selection. In fact, like the OSR, the PRR is an indirect measure of relative parental investment by each sex, where the sex providing greater parental investment will generally have a lower PRR. It is worth noting, however, that both measures can be influenced by other ecological and life-history variables, other than parental investment, with variable results for the strength of sexual selection (see below).

The ideas presented by Clutton-Brock and Vincent were expanded into a quantitative treatment by Clutton-Brock and Parker (1992). This spawned a wave of refinements, criticisms and tests, many of which drew heavily on sex-role-reversed species (e.g. Owens & Thompson, 1994; Simmons, 1995; Okuda, 1999; Masonjones & Lewis, 2000; Berglund & Rosenqvist, 2003; Sogabe & Yanagisawa, 2007). Most importantly, Ingrid Ahnesjö, Charlotta Kvarnemo and colleagues noted that the relationships between the PRR, the OSR and sexual selection are not always straightforward, and can be sensitive to ecological

factors (Kvarnemo & Ahnesjö, 1996; Ahnesjö *et al.*, 2001). For instance, if males require particular resources (e.g. nest sites) to breed, then resource availability can constrain the proportion of breeding males. This can lead to mating competition among females, even when male PRR is higher. Males of the peacock blenny (*Salaria pavo*), for example, provide parental care inside rock crevice nests. Almada and colleagues (1995) found that females of this species competed strongly for mates in a population where nesting sites were extremely limited, such that only a small proportion of males were able to breed (Ahnesjö *et al.*, 2001). The translation of sex differences in PRR to differences in mating competition thus requires a consideration of which individuals are 'qualified to mate', as well as other important variables such as the adult sex ratio. Kvarnemo & Ahnesjö (1996) also argued for a reconceptualization of the PRR as the maximum reproductive rate of an average individual in the (perhaps hypothetical) scenario where that individual is provided with mates *ad libitum*. This differs substantively from Clutton-Brock and Vincent's (1991) original definition, which emphasized the *individual* with the maximum reproductive rate. Species with unusual sex roles were pivotal in testing and refining these new ideas (Okuda, 1999; Masonjones & Lewis, 2000; Berglund & Rosenqvist, 2003; Forsgren *et al.*, 2004; Saraiva *et al.*, 2009; Safari & Goymann, 2021). For example, studies involving the broad-nosed pipefish, *Syngnathus typhle*, have demonstrated that a female, on average, can produce far more eggs than an average male can brood during the course of the breeding season, resulting in competition among females for the limited brood-pouch space (Berglund *et al.*, 1989). Interestingly, potential reproductive rates of the sexes vary with body size and water temperature (Berglund & Rosenqvist, 1990; Ahnesjö, 1995), providing avenues through which demographic and environmental variation can modulate the strength of sexual selection.

THE QUANTIFICATION OF MATING SYSTEMS AND SEXUAL SELECTION

The idea that patterns of mating have something to do with sexual selection, like so many ideas in the field, traces back to Darwin, who argued 'That some relation exists between polygamy and the development of secondary sexual characters, appears nearly certain; and this supports the view that a numerical preponderance of males would be eminently favourable to the action of sexual selection' (Darwin, 1871). The term polygamy, here, refers to any non-monogamous mating system, so polygyny (multiple

mating by males but not females), polyandry (multiple mating by females but not males) and polygynandry (multiple mating by both sexes) would all be different types of polygamy. This quote also highlights Darwin's engagement with the OSR concept.

If the mating system has something to do with the operation of sexual selection, then it should be quantifiable, and Angus Bateman (1948) was the first to tackle this problem. In a study far ahead of its time, he assigned parentage in captive populations of the fruit fly *Drosophila melanogaster* by scoring visible mutations that were known to be inherited in a Mendelian fashion. Bateman observed that offspring number was more variable in male than in female flies. He argued that this stemmed from two main causes: (1) males have greater variance in their number of mates than females; and (2) males have a stronger correlation between their number of mates and their number of offspring than females. Although Bateman's study was flawed in many ways, from the parentage methodology to the statistical analysis (Snyder & Gowaty, 2007; Gowaty *et al.*, 2012), it illustrated many important features of mating patterns, and played a major role in Trivers' treatment of parental investment. From the 1970s to the 1990s, Bateman's ideas were developed into formal metrics of mating systems with explicit, mathematical connections to selection theory. This resulted in the codification of the opportunity for sexual selection (the variance in relative mating success, defined as an individual's number of matings or mating partners); the opportunity for selection (the variance in relative reproductive success, defined as the number of offspring produced in a given time period); and the Bateman gradient (the slope of the regression of reproductive success on mating success) (Wade, 1979; Wade & Arnold, 1980; Arnold & Duvall, 1994; reviewed in Jones, 2009; Henshaw *et al.*, 2016, 2018; Anthes *et al.*, 2017).

Although Bateman himself was not strongly influenced by sex-role-reversed taxa, the widespread acceptance of mating system metrics was catalysed by key experiments in a sex-role-reversed species. If Bateman's logic applies to sex-role-reversed taxa, we would expect his key observations to be reversed. That is, females should have higher variance in mating and reproductive success, as well as a stronger correlation between mating and reproductive success, than males. These predictions were first tested in captive populations of the broad-nosed pipefish, *Syngnathus typhle* (Jones *et al.*, 2000, 2005). The experimental design was similar to Bateman's; however, the rise of modern molecular markers and statistical approaches alleviated the most serious shortcomings. The results showed that, indeed, this sex-role-reversed species was reversed

with respect to its mating system metrics, leading to a new, sex-neutral view that the sex experiencing stronger pre-mating sexual selection will have larger values for the opportunity for sexual selection, the opportunity for selection and the Bateman gradient. Further refinements show that the maximum value of a selection differential (s' ; in units of phenotypic standard deviations) acting on a sexually selected trait is equal to the product of the Bateman gradient (β_{ss}) and the square root of the opportunity for sexual selection (I_s): $|s'| \leq \beta_{ss} \sqrt{I_s}$ (Jones, 2009; Henshaw *et al.*, 2016, 2018; Henshaw & Jones, 2019). Subsequent work in sex-role-reversed species has strongly supported the utility of Bateman-inspired metrics, both as summary statistics of mating patterns and as predictors of sex differences in sexual selection (Fritzsche & Arnqvist, 2013; Henshaw *et al.*, 2016; Janicke *et al.*, 2016; Anthes *et al.*, 2017; Hare & Simmons, 2020).

The literature on mating system metrics focuses heavily on pre-mating sexual selection, rather than on post-mating processes like competition among sperm or eggs for fertilizations [for exceptions see e.g. Rose *et al.* (2013); Evans & Garcia-Gonzalez (2016); Marie-Orleach *et al.* (2016); Marie-Orleach *et al.* (2020)]. Post-mating sexual selection can nonetheless be analysed using analogous metrics, which are sex-neutral in principle. Importantly, however, there is limited potential for post-mating sexual selection on females of most species, even in those cases where mating competition is stronger in females. For instance, in species with internal fertilization within the mother, the eggs of multiple females have no opportunity to compete with one another for fertilizations. Unlike sperm competition, 'egg competition' is consequently not a selective force when fertilization occurs within the female. The situation is potentially more complex in species with external fertilization. If multiple females spawn in close proximity, then their eggs may theoretically compete with one another for fertilizations. However, since sperm greatly outnumber eggs, sperm competition will still generally be far more intense than competition among eggs. Egg competition may nonetheless be of evolutionary importance in some sessile broadcast spawners (Parker *et al.*, 2018). In addition, eggs may compete within the male brood pouches of syngnathid fishes (Paczolt & Jones, 2010). However, much of this competition occurs after fertilization (e.g. via selective abortion or differential resource allocation) and so might not be seen as sexual selection under some definitions. We believe that there is substantial room for improvement in the rigorous and sex-neutral application of Bateman-style metrics to post-mating sexual selection. Sex-role-reversed species would provide particularly useful test cases here.

SEX-ROLE REVERSAL AND A BALANCED VIEW OF THE SEXES

We have come a long way since the early days of 'undiscriminating eagerness' in males and 'discriminating passivity' in females (Bateman, 1948). We now appreciate that mating behaviour is much more complex and nuanced, with considerable variation in sex roles across and often even within species (Gowaty, 2003; Roughgarden, 2009; Janicke *et al.*, 2016; Amundsen, 2018; Hare & Simmons, 2020). In particular, we have learned that females often compete for mates and males can be choosy, even in species with largely typical sex roles (Hrdy, 1986; Amundsen, 2000; Bro-Jørgensen, 2007; Clutton-Brock, 2007, 2009; Kraaijeveld *et al.*, 2007; Bonduriansky, 2009; Rosvall, 2011). This diversification of thinking owes much to sex-role-reversed taxa, which, by their very existence, suggest a continuum of sexual selection in both males and females, and even the possibility that sexual selection could operate strongly or weakly in both sexes simultaneously.

Ultimately, this broader view of the sexes has moved into the mainstream, cemented in part by the inclusion of work on sex-role-reversed organisms into most textbooks on evolution and animal behaviour (e.g. Davies *et al.*, 2012; Futuyma & Kirkpatrick, 2017). The astonishment that once accompanied the news of male pregnancy in syngnathid fishes has been replaced with a knowing nod. That sex-role reversal has become part of the collective biological wisdom means that no one is surprised that females can be aggressive, active in courtship, ornamented or anything else that George Williams considered 'masculine'. If females can take on all of these roles in sex-role-reversed species, then it is not implausible that they might take on some of these roles in species with sex roles that were historically considered typical. Further, any trait historically associated with femaleness could potentially also evolve in males (Franklin-Hall, 2020).

In fact, we have come far enough in thinking about male and female roles in sexual selection that one could make a case that the term 'sex-role reversal' has outlived its usefulness. Ah-King and Ahnesjö (2013) tackle this question and conclude that the time to bury the term has indeed arrived. They point out four flaws in the term: (1) it is typological and reinforces stereotypical views of the sexes; (2) it divides nature into two categories, vastly simplifying the differences and similarities between the sexes; (3) it encourages a generalization that narrows the kinds of questions we can ask; and (4) it has broader meaning in society that is often at odds with its meaning in scientific applications. These flaws are real, and, as a consequence, scientists find themselves defining 'sex-role reversal' every time they invoke it.

Aside from identifying a research community, the main benefits of the terminology seem to be that it facilitates eye-catching titles for scientific papers, and, once defined, reduces slightly the number of words required to discuss species with non-typical sex roles. These benefits do not seem to be sufficient to make up for the problems. We believe that ‘sex-role reversal’ will continue to serve as a useful organizing banner; however, we urge researchers to be more explicit about what specifically is unusual about their study species (e.g. ‘female-biased mating competition’, ‘male-biased parental investment’, ‘males are choosier than females’ and so forth).

In closing this section, we would like to reiterate that, while sex-role-reversed taxa have had a disproportionate effect on the development of sexual selection theory, such taxa are by no means common. Even though sexual selection is vastly more complex than early treatments implied, the majority of species adhere to something akin to ‘conventional’ sex roles. In the vast majority of species, only females contribute resources towards offspring. Even in species with male care, female parental investment, including egg production, typically remains higher than that of males. As a consequence, in those species in which sexual selection is evolutionarily important, it is almost always stronger in males (Janicke *et al.*, 2016). Thus, the idea that the sexes form a perfectly symmetrical continuum is as inaccurate as naïve stereotypes about male and female roles. Despite their rarity, sex-role-reversed species have made an outsized contribution to our understanding of the origins, diversity and continued coevolution of sex roles in the natural world.

THE FUTURE OF SEX-ROLE REVERSAL

Unsurprisingly, we do not expect the impact of sex-role-reversed organisms on the conceptual development of sexual selection theory to end now. Recent theory has emphasized the coevolution of parental care and mating competition in both sexes, and the potential roles for ecological factors in guiding such coevolution (e.g. Klug *et al.*, 2013; Fromhage & Jennions, 2016; Lehtonen *et al.*, 2016; Royle *et al.*, 2016; Henshaw *et al.*, 2019; Iyer *et al.*, 2020). This theory will be most easily tested using comparative methods in clades with variable sex roles. Work in plovers of the genus *Charadrius* has already shown the great potential of this approach (Eberhart-Phillips *et al.*, 2017; Székely, 2019). Further comparative work (e.g. in shorebirds or the pipefish family Syngnathidae) will likely reveal insights that could not be gained by studying clades with more uniform sex roles. Thus, sex-role-reversed species will play a major role in continuing efforts to understand the evolution of mating systems, especially

as new work incorporates more realistic models of ecological, demographic and life-history variables.

Alongside research on interspecific variation, detailed studies of sex-role lability within species will be essential to refining our understanding of mating-system evolution (Ah-King & Gowaty, 2016; Hare & Simmons, 2020). Such plasticity is interesting in itself and is still poorly understood from an evolutionary perspective. We might expect plasticity in sex roles to evolve when mate availability fluctuates within or between generations (e.g. due to underlying environmental variation), such that both sexes are sometimes in short supply as mating partners. On the other hand, highly fixed sex roles might evolve when one sex is consistently over-represented in the mating pool. We see two potential caveats to such general expectations. First, traits that evolved primarily in non-mating contexts might be plastically cross-applied under ecologically unusual circumstances. For instance, a general cognitive module for ‘competing over scarce resources’ might be activated when mating partners become scarce, even in species where this circumstance is highly unusual. Second, some ‘sex-specific’ traits may in fact be expressible in either sex given appropriate stimuli (Hare & Simmons, 2020). For instance, choosiness in response to an abundance of available mates may often be a shared trait that is expressed more strongly in one sex than the other due to a combination of ecology and sex-specific life history (e.g. adult sex ratios, parental investment). Such hidden plasticity is perhaps more likely for cognitive and behavioural traits than for morphological traits like ornaments, which are often more closely tied to sex-specific developmental pathways.

Further, recent developments in genomics and transcriptomics have given us unprecedented power to resolve the effects of sexual selection on the genome. These new methods have already revealed intriguing patterns of genome evolution in a wide variety of taxa. Rigorous tests of how sexual selection shapes these patterns call for comparisons among lineages that differ in sexual selection intensity but are otherwise highly similar [for a trailblazing example, see Schumer *et al.* (2011)]. These conditions are epitomized by clades with highly variable sex roles, to which the majority of sex-role-reversed species belong. For instance, sex-role-reversed sandpipers, jacanas and phalaropes are nested within a larger radiation consisting primarily of species with conventional sex roles (Gibson & Baker, 2012). Similarly, the fish family Syngnathidae contains multiple independent evolutionary transitions from weakly sexually selected monogamous lineages to strongly sexually selected polygamous lineages (Wilson *et al.*, 2003). Patterns of genome evolution during these transitions could be very illuminating in terms of the genome-level

effects of sexual selection in general, as well as the specific effects that accompany the evolution of sex-role reversal.

Application of these genomic approaches to sex-role-reversed species will also reveal novel insights into sexual conflict. Intralocus sexual conflict arises when an allele is advantageous in one sex but deleterious in the other (Chippindale *et al.*, 2001; Bonduriansky & Chenoweth, 2009). Such genes should be particularly common in strongly sexually selected species, where alleles that enhance competitive ability will be under strong selection in one of the sexes. These alleles are generally expected to be deleterious in the other sex, resulting in conflict. Over evolutionary time, selection favours a resolution of this conflict, possibly by the evolution of sex-specific expression (Rice, 1984; Emlen *et al.*, 2006; Rowe *et al.*, 2018). Examination of this process in sex-role-reversed species could be especially interesting, as the mechanisms resulting in female-specific expression of alleles favoured by sexual selection could be different than those resulting in male-specific expression in species with conventional sex roles. For instance, a gene can evolve to have sex-specific expression by being put under the direct or indirect control of the sex-determination hierarchy (Billeter *et al.*, 2006; Meeh *et al.*, 2021) and in vertebrates this process is mediated mainly by androgens, oestrogens and their receptors (Mougeot *et al.*, 2004; Blas *et al.*, 2006; Anderson *et al.*, 2020). Indeed, initial work on the endocrinology of sex-role-reversed taxa was motivated by the hypothesis that circulating levels of sex steroids would be reversed between the sexes (Rissman & Wingfield, 1984; Mayer *et al.*, 1993); however, these early studies and more recent results have demonstrated that the situation is much more complex and nuanced (Eens & Pinxten, 2000; Lipshutz & Rosvall, 2020). For example, certain regions of the brains of female black coucals and barred buttonquails appear to have evolved enhanced responsiveness to androgens (Voigt & Goymann, 2007; Voigt, 2016). In addition, progesterone appears to play a major role in territorial aggression in black coucal females (Goymann *et al.*, 2008). Additional examples, none of which represents a wholesale reversal of the endocrine system, can be found in the recent comprehensive review of this topic by Lipshutz and Rosvall (2020). Although no general, proximate mechanism underlying sex-role-reversed behaviour and morphology has yet emerged, future investigations into the idiosyncrasies of sex-role-reversed species will no doubt shed additional light on the evolution of sex differences in terms of behaviour, physiology and the genome-level effects of intralocus sexual conflict.

In addition to intralocus sexual conflict, we expect interlocus sexual conflict to be important in species experiencing strong sexual selection (Arnqvist &

Rowe, 2005). In such cases, conflict arises because the reproductive interests of the two sexes do not completely align, leading to selection for one sex to evolve adaptations to manipulate the reproductive activities of the other sex (Rice & Holland, 1997; Chapman *et al.*, 2003). The target will then evolve adaptations to circumvent the manipulations, resulting in an arms race between the sexes. A well-known example of this type of arms race is the evolution of male accessory gland proteins in *Drosophila*, which are transferred to the female during copulation and enhance short-term female fecundity, exacting a cost in terms of a shorter lifespan (Chapman *et al.*, 1995). Similar processes could be involved in sex-role-reversed species, if sexually selected females are capable of evolving traits that allow them to manipulate the reproductive behaviour or physiology of males. Obvious candidates for interlocus sexual conflict are the pipefishes (Paczolt & Jones, 2010), in which females transfer ovarian fluid along with their eggs into the male's brood pouch.

Finally, progress in evolutionary biology often depends on the development of tractable laboratory systems, and here we feel that sex-role-reversed species still offer much untapped potential. The most famous and best-studied examples of sex-role reversal occur in birds and fishes. Most of these vertebrate species do not have favourable characteristics for establishment as laboratory models. Of all sex-role-reversed vertebrates, the most tractable as model systems are probably the seahorses and pipefishes, which can be held in large numbers in relatively small aquarium tanks. In addition, some species appear to have a relatively short generation time, reaching sexual maturity after a few months. Perhaps even greater promise is offered by sex-role-reversed insects, which have numerous characteristics, such as small body size and short generation times, that make them more tractable than most vertebrates. For instance, honeylocust beetles of the genus *Megabruchidius* have proven a robust and practical model system, with manageable breeding requirements and generation times short enough to perform experimental evolution (Bookmythe *et al.*, 2014; Fritzsche *et al.*, 2016), which represents yet another tool for studying sex-role reversal that could prove to be profitable in the near future. The seed beetle subfamily (Bruchinae), to which *Megabruchidius* belongs, also contains many species with more typical sex roles (e.g. the well-studied agricultural pest *Callosobruchus*), providing a promising avenue for comparative work (Fritzsche & Arnqvist, 2013). Many other insect species have life histories suggestive of sex-role reversal and could reward the ambitious researcher seeking to develop a new laboratory system [for inspiration see Requena *et al.* (2014); Hare & Simmons (2020)]. Eventually, the application of functional genomic tools, such as CRISPR/Cas9 (Doudna & Charpentier, 2014), could revolutionize our

understanding of the mechanisms underlying sex-role-reversed traits and behaviours. As comparative studies continue to reveal the endocrinological and genomic basis of sex-role reversal, potential targets for more detailed investigation will continue to emerge, and functional genomics approaches appear to be a logical next step. Once tractable sex-role-reversed laboratory models are established, only minor logistical hurdles, such as perfecting methods for microinjection into early-stage embryos, stand in the way of functional genomic applications in the study of sex-role reversal.

CONCLUSIONS

Charles Darwin laid the foundations for the study of sex-role-reversed species 150 years ago with his natural history observations of barred buttonquails, emus, phalaropes and other birds. He even showed a glimmer of understanding regarding the significance of such taxa for his theory of sexual selection. Modern researchers took up the cause, and sex-role-reversed species played a major role in a series of conceptual breakthroughs that have revealed links between ecological factors, mating systems and sexual selection intensity. Initially, sex-role-reversed species mainly served as fodder for thought experiments by fertile minds. Eventually, however, they became subjects of careful study, resulting in a much richer field of sexual selection research than would have been possible had such species never evolved. Amazingly, the thread of Darwin's original ideas has remained intact throughout this enterprise. We look forward to a future in which we understand sex-role reversal much better than we do today, and we are certain that such understanding will enlighten the study of sexual selection in ways we have yet to imagine.

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