

# Sexual Selection and Female Competition

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Advanced article

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**Sexual selection studies have traditionally focused on reproductive competition as a typical male characteristic, and regarded females as largely passive. However, empirical evidence now shows female competition to be widespread in nature. Sometimes the same conventional logic can be used to explain competitiveness in males and females: that the sex in surplus in the mating pool has to compete for the other sex as a limited resource. Still, female competition often does not follow this pattern. This is partly related to the fact that whereas the obvious target of male competition is usually access to mates, in females, competition for mating opportunities is often intertwined with competition for breeding resources. Rather than assuming a rigid dichotomous view of sex roles focusing on which sex is more competitive, the topic may be more rewardingly approached by identifying how ecology affects costs and benefits of competitiveness in the two sexes separately.**

‘Sexual selection of a trait can [...] be viewed as a shorthand phrase for differences in the reproductive success, caused by competition over mates, and related to the expression of the trait’

Andersson, 1994

## Introduction

The ubiquitous force of male mate competition in the animal world has been a prime target of the zoological research inspired by Darwin’s ideas. The manifestation of male competition is often conspicuous, be it as dramatic weapons or exaggerated body size, and Darwin coined

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the term ‘sexual selection’ specifically to account for the extreme male phenotypes, which had evolved as a consequence of competition for mates (Darwin, 1871). However, evidence is increasing that also females often compete, although the manner in which they do so tend to be more discrete. Here I will first examine the causes underlying the general differences in sex roles between males and females. On this basis I will then focus on the factors which promote female competition, both in the context of sex role reversal and in the context of otherwise conventional sex roles. We will see that whereas mates are typically the obvious target of male competition, the basis for female competition can be more difficult to disentangle and often relates to mate quality and access to breeding resources. Adopting a simplistic, stereotypic notion of sexual selection, rather than understanding the proximate and ultimate causes underlying selection on sex roles in specific cases, therefore precludes a deeper understanding of biological diversity. See also: [Evolution: History](#)

## How Conventional Sex Roles are Shaped by Sexual Selection

Males are distinguished from females based on the smaller size of their gametes. However, generally there are several other traits, which tend to be more pronounced in males than females, and vice versa. Notably, males are often more aggressive in assuring access to mates whereas females tend to be more discriminative in mate choice as well as more prone to care for offspring. Why is it so? A simple logic observes that since males invest less in each reproductive event, they will sooner be ready to mate again, and more males than females are therefore available to mate at a given time. In other words, the operational sex ratio (OSR), which is the ratio of ready-to-mate males to ready-to-mate females, becomes male-biased (Emlen and Oring, 1977). As a consequence, males are seen as the limited sex that has to compete for a limiting resource, females.

However, this logic does not clearly answer the question as to why males struggling to find a mate are not selected to invest more in parental care rather than in competitive traits: because it is more difficult for males to acquire another mate, we could expect that males would be more

likely than females to invest in offspring (Jennions and Kokko, 2010). Likewise, we could expect that it would be more beneficial for females rather than males to seek additional mating opportunities as they would more easily find a mate (Jennions and Kokko, 2010). Following a similar logic to that used to explain equal primary sex ratios (Fisher, 1930), we could indeed expect the OSR to approach unity, with the sex in surplus always benefitting more from providing care rather than from seeking additional mating opportunities. Why this does not happen can be attributed to the fact that selection promotes traits that are beneficial to the most successful individuals rather than the average individual.

To understand why male care is not more common, we therefore need to consider tradeoffs consequential to sexual selection for competitiveness in the most successful males. Because males typically invest less than females in each mating event, they generally have the highest potential reproductive rate, that is the maximum rate of offspring production under (hypothetical) unlimited access to mates (Clutton-Brock and Vincent, 1991). This favours stronger variance in actual reproductive rates in males, which equates a higher opportunity for sexual selection on males (Wade, 1979). If the variance in actual reproductive rates is random, no trait selection takes place (Sutherland, 1985). However, often certain traits increase male reproductive success either by increasing competitiveness or attractiveness. If these traits have a heritable basis, they evolve by sexual selection. Such competitive and attractive traits are often costly and tradeoff against investment in offspring, so that their evolution selects against paternal care. The point here is that we should not regard patterns in parental investment as a precondition but consider how parental investment interacts dynamically with sexual selection on other traits, in order to arrive at a deeper understanding of why males generally are more competitive and more displaying, but less caring than females (Jennions and Kokko, 2010). **See also:** [Parental Care and Investment](#); [Post-fertilization Reproductive Strategies](#)

Another factor that selects against paternal care is that males in many taxa are less certain of paternity than females. Indeed one of the major insights in the field of sexual selection in more recent times is that promiscuous mating by females is widespread in species with internal fertilisation, notably in mammals, birds and reptiles (Zeh and Zeh, 2003). Hence, in contrast to females, who are generally able to allocate care exclusively to own offspring, a proportion of male parental care will often inadvertently be directed at the offspring of others. Males therefore have a stronger incentive than females to invest in additional matings rather than parental care.

What then explains patterns in mate choice? Choosiness basically provides benefits by increasing mate quality at a cost that is ultimately associated with a reduced mating rate. A decrease in mating rate typically has less negative fitness consequences for females than for males because of their shallower 'Bateman gradient' (i.e. the slope of the curve describing reproductive rate as a function of mating

rate, Bateman, 1948), and this can explain why females are often more choosy. Choosiness is furthermore disfavoured in the most competitive sex, because restricting the number of acceptable mating partners would intensify already costly competition. Still, where mate quality has important fitness consequences, competition and choosiness can co-exist in the same sex as a high cost–high benefit strategy (see below). **See also:** [Precopulatory Reproductive Strategies](#); [Sexual Selection](#)

## Female Competition and its Possible Evolutionary Causes

Given the forces promoting competitiveness as a male sex role and choosiness as a female sex role, how can we understand the empirical observations of female competition? Firstly, I will examine the extreme cases of sex role reversal where females are more competitive than males. However, it is important to realise that competitiveness (or choosiness) in one sex does not preclude it in the other. To stress this point, I will therefore go on to consider causes of female competition in species where the conventional sex roles otherwise predominate.

### Reversal in competitive roles under female-biased OSR

Reversal in the pattern of parental care is often regarded as a precondition for reversal in competitive roles to occur (Andersson, 2005). There are several examples of animal taxa in which males provide more parental care than females, notably among invertebrates, fishes, amphibia and birds (Ridley, 1978; Andersson, 2005). This underscores the point made above, that it is not anisogamy *per se* that selects for maternal care but rather investment in parental care is influenced by tradeoffs with other fitness-related traits that depend on anisogamy, in particular competitiveness. It is indeed a widespread misconception that females invest more in care simply because they stand to lose a larger historical investment in gametes. This flawed logic commits the Concorde fallacy by assuming that the optimal strategy for the future depends directly on past investment (Kokko and Jennions, 2008).

Which conditions favour male care? In many cases the evolutionary origin of paternal care is still not very clear but it appears that the crucial ecological and life history factors differ between taxa. In some cases, male care seems consequential to a male-biased adult sex ratio. Hence although both birds and mammals typically have a male-biased OSR, the adult sex ratio is generally biased towards males in birds (owing to high mortality of breeding females) but towards females in mammals (owing to high mortality in male competition; Andersson, 2005; Kokko and Jennions, 2008). This may cause stronger selection

for male care in birds: more competitors increase the cost:benefit ratio of investment in competitive traits, and attenuated selection for competitiveness in turn increases the scope for investment in male care. In fishes, male care may have evolved because tradeoffs with competitiveness are relatively weak: defending and aerating eggs is reasonably compatible with the defence of nest sites for spawning females (Reynolds *et al.*, 2002).

Once male care has evolved, females must produce more eggs than males can care for before the OSR becomes female-biased (Andersson, 2005). Favourable resource conditions are likely to favour this shift. Under these circumstances competitive traits are likely to be advantageous to females and polyandry can evolve. The underlying logic is similar, but reverse, to the one used to explain conventional sex roles above. However, note that in many species where male care predominates, males are also the more competitive sex. The usefulness of the OSR in understanding exactly when role reversal in competition occurs is illustrated by the example of the two-spotted goby, *Gobiusculus flavescens* (Figure 1) (Forsgren *et al.*, 2004). In this fish, males defend nest sites in brown algae or empty mussels. Females spawn in the nests and parental care is exclusively provided by males, which clean the nests and fan and defend the eggs. In the beginning of the season, the OSR is male-biased and both intrasexual competition and courtship behaviour are most pronounced in males. However, over the season male abundance declines 10-fold, probably owing to exhaustion from parental care and intrasexual competition and/or higher rates of infections and predation. Since the female population remains stable, the OSR becomes female-biased and at the end of the season, female competition and female courtship predominate.



**Figure 1** A male (below) and a female two-spotted goby showing their courtship displays while swimming in parallel. Over the breeding season, female competition increasingly replaces male competition as high male mortality takes its toll. Photo by Elisabet Forsgren (reproduced from Amundsen and Forsgren, 2001). Copyright (2001) National Academy of Sciences, USA.

## Reversal in competitive roles not predicted by the OSR

The OSR may often be helpful in explaining when competition is stronger in females than in males; however, this is not always the case. Although a male-biased OSR is expected to promote higher variance in male reproductive success and thereby stronger selection for competitiveness, the intensity of selection on competitive traits also depends on their effectiveness in monopolising reproduction, which in turn depends on ecology and life history. For example, where resources are scarce, females may benefit more by suppressing the reproduction of others to secure breeding resources than males stand to benefit from mate competition. A case in point is the meerkats *Suricata suricatta* in the Kalahari Desert. The shortage of breeding resources in their harsh environment has led to a cooperative breeding system where reproduction is monopolised by a single breeding pair in colonies of up to 50. Although females are the primary care givers and the OSR is male-biased, dominance is associated with higher reproductive benefits in females than in males (Clutton-Brock *et al.*, 2006). This is linked to longer tenures of dominant females relative to dominant males, possibly because reproductive suppression is most effective in females that primarily need to suppress immature natal competitors, male competition involving more confrontations with adult immigrants. Similarly in spotted hyenas *Crocuta crocuta* competition for dominance is stronger among females than males in spite of a male-biased OSR (Figure 2). A stronger effect of dominance on reproductive output can explain why female spotted hyenas have evolved to become larger and more aggressive than males (Holekamp *et al.*, 1996; Engh *et al.*, 2002).

These examples illustrate that the OSR is not an infallible predictor of sex roles and that different aspects of sex roles, such as competitiveness and parental care, do not have a simple one-to-one relationship; rather ecological conditions can lead to a variety of outcomes. This is also clear



**Figure 2** In hyenas, social rank is more closely linked to reproductive success in females than in males, and females are there larger and more aggressive than males. Photo by the author.

from the cases which we will consider next, where female competition occurs in species otherwise known for the intensity of male competition.

## Female mate competition in the context of conventional sex roles

It is important to recognise that female competitiveness can be selected whenever the benefits of competitive traits outweigh their costs, regardless of whether males are competitive or not. Female competition in species otherwise conforming to conventional sex roles is evident in cases of aggression towards the mating activities of others. Whereas the obvious benefit driving male competition for access to females is usually an increased number of fertilisations, the possible explanations for female mate competition in species without role reversal are more diverse. The possible benefits include increased conception probability (either in general or specifically with preferred males) and improved access to resources (either immediately or in the future).

### Competition for limited sperm

Although the relatively cheap male gametes are usually vastly more abundant than ova, constraints do apply to sperm production (Dewsbury, 1982; Wedell *et al.*, 2002). The relevance of such constraints is shown by considerable evidence that females do suffer sperm limitation under certain circumstances (Charlat *et al.*, 2007). In this situation, competitive traits which increase mating rate can be advantageous to females (Saether *et al.*, 2001). Factors promoting sperm depletion include (i) breeding synchrony, (ii) female mating biases, and perhaps most importantly, (iii) female promiscuity.

First, synchronised breeding, which can be advantageous in seasonal environments or where predation risk is high (Sinclair *et al.*, 2000), increases the demand for sperm during the mating season. It has indeed been suggested that chimpanzees *Pan troglodytes* avoid synchronising oestrus cycles to secure sperm availability (Matsumoto-Oda *et al.*, 2007). The effect of breeding synchrony on male availability is captured by the OSR, which becomes more female-biased during synchronised breeding seasons, favouring female competition.

Secondly, female mating biases, including mate choice in the broadest sense (i.e. as any female behaviour leading to a mating bias which reduces the number of mates available, Wiley and Poston, 1996), can in extreme cases limit the availability of sperm from popular males (Preston *et al.*, 2001). A shortcoming of the conventional OSR in this context is that it is based solely on quantity of mates and fails to capture the importance of variation in mate quality (Owens and Thompson, 1994). However, if only males 'qualified' to mate are considered in OSR calculations, female mating biases can be seen as essentially skewing the OSR towards a female-bias, thus promoting female competition (Ahnesjö *et al.*, 2001; Klug *et al.*, 2010).

Thirdly, where females are promiscuous and mate repeatedly with several males, the conventional OSR also becomes less meaningful in predicting competition in the two sexes. Focusing on the relative numbers of each sex available to mate makes less sense when mate acquisition no longer equals offspring production in either sex. In this case, additional matings may entail high payoffs to females by enhancing the probability of a high quality male winning in sperm competition (i.e. the competition between sperm of multiple males to fertilise the ovum; Parker, 1970). Although males also have an interest in increasing their odds in sperm competition, unlike females they are susceptible to opportunity costs of mating owing to sperm depletion. **See also:** [Postcopulatory Reproductive Strategies](#)

The topi antelope *Damaliscus lunatus* illustrates how female mate competition can emerge in the context of breeding synchrony, unanimous mating preferences, and female promiscuity (Figure 3). During a 6-week rut, females in heat move to mating arenas called leks. Although females mate repeatedly with several males during their one-day oestrus, they show a strong preference for males holding central territories on the leks. That sperm limitation is an issue is suggested by the facts that central lek males become visibly exhausted during mating peaks and oestrous females increase their mating probability by attacking mating pairs (Bro-Jørgensen, 2007).

### Indirect resource competition

Female reproductive success is often primarily determined by access to resources (Davies, 1991) and even where the immediate target of female competition is access to mates, the behaviour may actually reflect indirect resource competition. Hence males often monopolise resources to acquire mates (Clutton-Brock, 1989), and because males vary in their ability to defend resources, females may compete for mates with superior resource-holding potential. Such competition is mainly expected where strong limitations to male harem-size apply, such as in monogamous species (Stockley and Bro-Jørgensen, 2011). Arguably, this may be an important factor promoting competition between women in human societies (Campbell, 1999).

Rather than securing immediate access to resources, female mate competition may also be selected to prevent other females from reproducing and thereby improve access to resources in the future. Such an explanation is most likely where female groups are stable and of modest size, such that the offspring of others are plausible competitors for the female and/or her offspring in the future. There is currently little direct evidence linking female mating interference to reduction in the intensity of future resource competition. However, the presence of female-led infanticide strongly suggests that the offspring of others sometimes do constitute significant competitors (Stockley and Bro-Jørgensen, 2011).



(a)



(b)

**Figure 3** (a) Two female topi antelopes fighting on a mating arena ('lek'). (b) A female (in front to the left) attacks a male attempting to mate with another female (at the back). In topi, female mate competition occurs in a society that is otherwise dominated by intense male competition for central lek territories. Photos by the author.

## Conclusion

The study of reproductive competition in sexual selection has traditionally focused on males but robust empirical evidence of female competition now highlights the importance of considering competition in both sexes to understand the dynamics of sexual selection. A logic focusing on shifts in OSR may often, but not always, explain female competition where sex roles are reversed. However, that female reproductive competition is also widespread in species without role reversal shows the limitation of the OSR approach to understand diversity in sex roles. Thus, variation in mate quality and the availability of breeding resources may select for female reproductive competition also in species where conventional sex roles otherwise predominate. In many cases where the presence of competitive traits in females is undeniable, the ultimate cause is still not clear, but it appears that

important differences exist in the reproductive competition of the two sexes. In males the obvious target of competition is typically access to mates, but in females, the ultimate cause of reproductive competition may often relate to access to breeding resources. This has given rise to a debate as to whether sexual selection should be redefined to better encompass both sexes (see Carranza, 2009; Clutton-Brock, 2007, 2009; Stockley and Bro-Jørgensen, 2011). From an empirical point of view, there is need not only to focus on female competition in the extreme examples of sex role reversal, but also more studies are needed on the proximate and ultimate reasons for female competition in taxa with otherwise conventional sex roles under different ecology conditions.

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