Sexual Selection in Males and Females

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Research on sexual selection shows that the evolution of secondary sexual characters in males and the distribution of sex differences are more complex than was initially suggested but does not undermine our understanding of the evolutionary mechanisms involved. However, the operation of sexual selection in females has still received relatively little attention. Recent studies show that both intrasexual competition between females and male choice of mating partners are common, leading to strong sexual selection in females and, in extreme cases, to reversals in the usual pattern of sex differences in behavior and morphology.

In the *Descent of Man* (1871), Darwin provided the first coherent explanation of the elaborate weapons and ornaments found in males and, less commonly, in females in many animals. These "secondary" sexual characters did not appear likely to increase survival, and he argued that they were a result of intrasexual competition either for breeding opportunities or to attract the opposite sex. He termed this evolutionary process "sexual selection," describing it as selection that "depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction" (*1*, p. 209).

Our current understanding of Darwin's theory, based on seminal papers by Bateman (*2*) and Trivers (*3*), is that reduced investment in gametes and parental care by males increases their potential rate of reproduction (PRR) (*4*, *5*), biasing the relative numbers of sexually active males to receptive females at any one time (the operational sex ratio, or OSR) (*6*). Biased OSRs, in turn, lead to increased intensity of intrasexual competition, greater variance in breeding success, and stronger selection for traits affecting competitive ability in males than in females (*3*, *6*, *7*). In addition, they are likely to favor the evolution of greater selectivity in choice of mating partners by females, generating selection pressures in males for traits that display their quality as breeding partners (*3*, *8*). Where secondary sexual characters confer important reproductive benefits, they may develop to a point where their benefits are offset by substantial costs to survival, either among juveniles or among adults (*3*, *9*).

Although the assumptions and predictions of the theory of sexual selection have withstood repeated testing (*10*), recent reviews have pointed to inconsistencies in relationships between parental investment, reproductive competition, and sex differences in behavior and morphology, as well as to the scarcity of detailed studies of the operation of sexual selection in females (*11–15*). Roughgarden *et al*. (*16*) recently argued, in this journal, that "sexual selection theory is always mistaken, even when gender roles superficially match the Darwinian templates" and went on to advocate its replacement by a novel theory of social selection. That 40 evolutionary biologists cooperated to write 10 letters rejecting these criticisms shows that Roughgarden's views are unusual (*17*), but it is clear that the mechanisms underlying sex differences in reproductive competition and the traits associated with them are both more diverse and more complex than was initially realized. In the wake of Roughgarden *et al*.'s review, both the exceptions to the basic structure of sexual selection theory and the operation of sexual selection in females deserve further attention.

Sexual Selection in Males

It is now clear that relationships between relative gamete size, the evolution of parental care, OSRs, the relative intensity of competition, and the extent of selectivity in the two sexes are not as straightforward as was originally supposed. Sex differences in parental care are not an inevitable consequence of sex differences in gamete size because patterns of parental care are likely to coevolve and feedbacks may be complex (*18*, *19*). Sex differences in parental investment are not the only factors affecting the OSR (*5*, *15*): Biases in the sex ratio at birth or hatching, sex differences in juvenile or adult survival or in the proportion of individuals acquiring the resources necessary to breed, and variation in the costs of competing may all affect the relative numbers of males and females competing for mates in the two sexes (*5*, *20–22*). Finally, the OSR is not the only factor affecting the relative intensity of intrasexual competition and mate selection in the two sexes, and the sex that competes most intensely for breeding partners is not always less selective in its choice of mates. For example, the usual tendency for females to be more selective than males can be reversed where variance in female quality is large and males can increase their fitness by selecting superior partners (*13*, *23*, *24*).

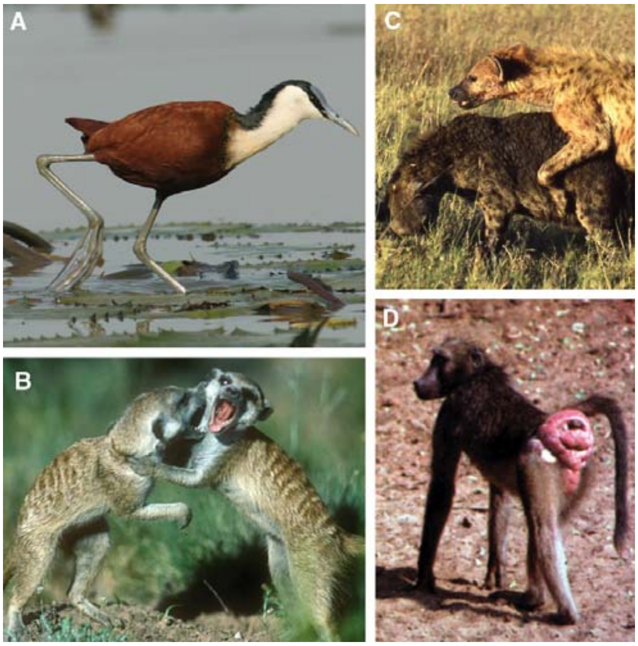

Fig. 1. In many animals, competition between females for breeding opportunities is intense, and females show pronounced secondary characters. In polyandrous birds, where males invest heavily in parental care, females compete intensely more frequently for breeding opportunities than males and are commonly larger than males as in (**A**) female African jacana (*Actophilornis africanus*). Female competition for breeding opportunities is also intense in a number of social mammals where female rank and breeding success are closely correlated, including (**B**) Kalahari meerkats (*Suricata suricatta*) and (**C**) spotted hyenas (*Crocuta crocuta*). Females have developed pronounced secondary sexual ornaments that attract males in some polygynous or promiscuous species, including (**D**) savannah baboons (*Papio cynocephalus*). In a number of birds, both sexes have similar ornaments probably as a result of mutual mate-choice, while in a few species, males and females display in different sites and have developed contrasting coloration. [Credits: (A and B) A. Young; (C) M. L. East and H. Hofer; (D) T. Clutton-Brock]

Relationships between intrasexual competition and reproductive variance are also more complex than early papers suggested. Although variance in fitness is a prerequisite for selection, a substantial proportion of reproductive variance in

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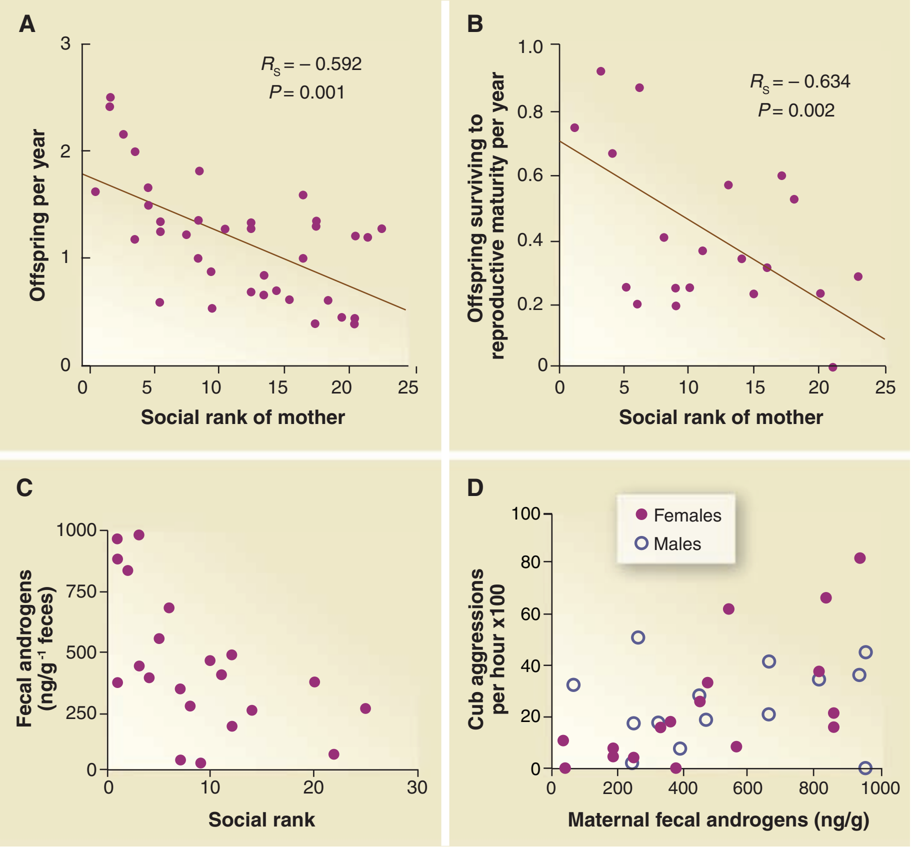

Fig. 2. Correlates of female rank in spotted hyenas. (**A**) Total number of offspring produced per year by the mother shown as a function of the social rank of the mother. (**B**) Number of offspring surviving to reproductive maturity produced per year as a function of the social rank of the mother. (**C**) The relationship between fecal androgens and social rank in female spotted hyenas during the second half of gestation. (**D**) The relationship between maternal androgens measured during the second half of gestation and rates of aggression in hyena cubs aged 2 to 6 months. [(A) and (B) reproduced from (*39*) by permission of the Society for Reproduction and Fertility (2007); (C) and (D) reproduced from (*43*) by permission]

both sexes is often caused by age, by random processes that do not contribute to selection, or by phenotypic differences that have no heritable basis (*7*, *13*, *14*, *25*–*27*), and these effects may often differ between the sexes. For example, the higher PRR of males may generate increased random variance in breeding success in males compared to females (*25*). In addition, because breeding success is often more strongly influenced by age in males than in females, calculation of relative variance in breeding success across individuals of unknown age often overestimates variance in male reproductive success and underestimates variance in female success (*7*).

Finally, relationships between relative reproductive variance in the two sexes and the evolution of sex differences are complex and inconsistent. Qualitative differences in the selection pressures operating in males and females are common, leading to the evolution of contrasting secondary sexual characters in males in different species (*7*). For example, in some polygynous shore birds, males fight on the ground, selection favors large body size, and males are larger than females, whereas in species where males compete in aerial displays, selection for agility favors small size in males and males are smaller than females (*28*). Similarly, in ungulates, where males fight in pushing contests, there is strong selection for male size and sexual dimorphism is pronounced, whereas in species where males fight by biting, body size does not increase the competitive ability of males and sex differences in body size are small (*7*). In other cases, sex differences in ornamentation are associated with qualitative differences in the selection pressures operating in males and females rather than with sex differences in reproductive variance. For example, in some birds, males and females compete at different sites and have developed contrasts in plumage color related to the sites where they display (*29*). Recent examples of sexual antagonism also provide further evidence of the importance of qualitative differences in the selection pressures operating on the two sexes (*27*, *30*, *31*). It is consequently unfortunate that more attention continues to focus on sex differences in reproductive variance than on differences in the selection pressures operating in males and females.

Sexual Selection in Females

Although secondary sexual characters are widespread in females (Fig. 1), Darwin paid little attention to them, noting in passing that "in almost every great class a few anomalous cases occur, where there has been an almost complete transposition of the characters proper to the two sexes; the females assuming characters which properly belong to the males" (*1*). Subsequent research on birds showed that a small number of shore birds have polyandrous mating systems, which generate female-biased OSRs, more intense reproductive competition among females than males, and greater development of secondary sexual characters in females (*3*, *6*). However, with the exception of polyandrous species, relatively little attention has been paid to the operation of sexual selection or the evolution of secondary sexual characters in females.

Intense reproductive competition among females is not confined to species where males invest more heavily than females in their offspring and OSRs are biased toward males and is widespread in species where males are the principal competitors. Sexual selection operating in females may reduce the degree of sexual dimorphism, in some cases leading to monomorphism. For example, in a number of birds where females and males have similar ornaments, both sexes are commonly involved in aggressive displays with rivals, indicating that intrasexual competition may be involved (*32*, *33*). In a small number of animals, the resources necessary for successful breeding in females are so heavily concentrated that reproductive competition between females is more frequent or more intense than between males, despite greater investment in parental care by females (*34*). Examples include several cooperative breeders where a single female monopolizes reproduction in each group and her offspring are reared by other group members (*32*, *35*, *36*) as in Kalahari meerkats (*Suricata suricatta*), where females invest more heavily in parental care than males but depend on access to groups of nonbreeding subordinates to rear their young (*37*). Fewer females than males breed as dominants, and variance in breeding success is higher in females than in males (*34*). In naked mole-rats (*Heterocephalus glaber*), breeding females suppress reproduction in other females, evicting or killing challengers, and are larger and more frequently aggressive than other group members and dominant to males (*38*). More intense intrasexual competition among females than males also occurs in some mammals where multiple females breed in each group. For example, in spotted hyenas (*Crocuta crocuta*), females compete intensely for social rank, which is closely related to their breeding success (Fig. 2) (*39*).

In many species where females compete intensely for breeding opportunities, they show unusual behavioral, physiological, or anatomical characteristics. Female meerkats are more frequently aggressive to each other than are males, and their body weight has a stronger influence on their chances of acquiring and maintaining dominant status (*34*). Both in meerkats and in naked mole-rats, females that attain dominant status show elevated levels of testosterone at particular stages of the reproductive cycle, as well as a secondary period of growth (*40*, *41*). Heightened testosterone levels in breeding females also occur in spotted hyenas (*42*, *43*) and in some lemurs (*44*, *45*), as well as in some breeds of domestic cattle where females have been selected for competitive ability (*46*). In a number of these species, the genitalia of females show evidence of masculinization (*44*, *45*, *47*, *48*) while, in the cooperative cichlid fish (*Neolamprolagus pulcher*), not only are testosterone levels consistently higher in dominant females than in subordinates, but the brain gene expression profiles of dominant females resemble those of males (*36*).

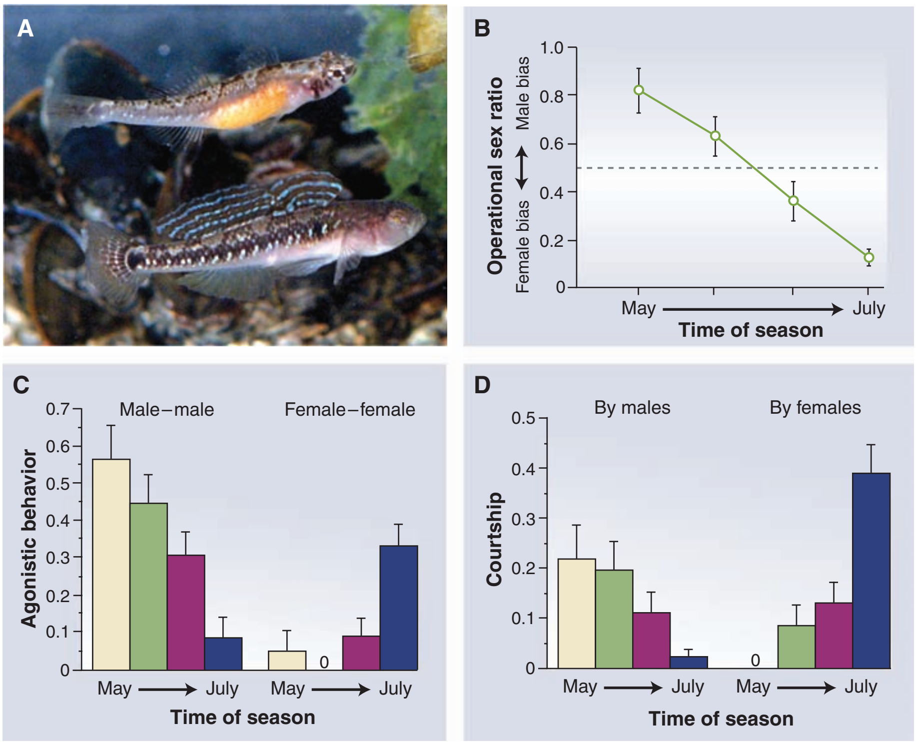

Fig. 3. Seasonal changes in the relative frequency of competition and display in two-spotted gobies (*Gobiusculus flavescens*) [reproduced from (*66*) by permission]. (**A**) Female and male two-spotted gobies. (**B**) Seasonal changes in the operational sex ratio. (**C**) Change in male and female propensity to behave agonistically when encountering same-sex individuals. (**D**) Change in male and female propensity to perform courtship.

Male mate choice is also widespread in species where OSRs are male-biased and is often associated with female courtship of males as well as with the evolution of conspicuous sexual ornaments in females. In some cases, female ornaments reflect individual differences in fecundity and males prefer highly ornamented partners (*21*, *49*, *50*). For example, in some empidid dance flies where males provide nuptial gifts for females, females have developed enlarged pinnate leg scales that honestly reflect their fecundity and males choose females with large leg scales (*51*). Fat-padded breasts, thighs, and buttocks in human females may have evolved for similar reasons (*52*). In other cases, female ornaments appear to reflect temporal changes in reproductive status. In some primates that live in groups where females have an opportunity to mate with more than one male, females show pronounced swellings of the perineal region that are largest and brightest around the time of ovulation and attract the attention of males (*53*, *54*). The relative size of sexual swellings differs between females, so these differences may also signal individual variation in reproductive performance (*55*). Mutual mate choice by males and females also occurs in a number of monogamous birds and, like intrasexual competition, may lead to the evolution of similar ornaments in males and females (*24*, *49*, *56*).

Where both sexes invest heavily in their progeny, the OSR and the relative intensity of breeding competition in the two sexes sometimes vary throughout the reproductive cycle. In some fish, intense male:male competition and frequent male displays at the beginning of the season are replaced by active competition between females for males and female displays as the season progresses (Fig. 3). Similarly, in some polygynous ungulates where males initially compete intensely for females, females that have entered estrus and need to mate rapidly compete for the attentions of defending males (*57*, *58*). Several studies of species where both sexes make large investments in their offspring have shown that the relative intensity of reproductive competition in the two sexes can be changed by manipulating resource availability and reversing sex differences in PRR (*59*, *60*).

Contrasts in the Operation of Sexual Selection in Males and Females

Although intrasexual competition for breeding opportunities and consistent mating preferences in the opposite sex appear to have played an important role in the evolution of secondary sexual characters in both sexes, there are fundamental differences in the operation of sexual selection in males and females. Because of their greater energetic investment in gametes and parental care, females more commonly compete with each other for access to resources necessary for successful reproduction (including breeding sites, parental care, and social rank) than for access to gametes produced by the opposite sex (*33*, *34*). As a result, the relative intensity of intrasexual competition and the development of traits that increase competitive success in females may be more strongly influenced by differences in resource distribution than by variation in mating systems. Intrasexual competition between females for resources may generate large individual differences in fecundity (*61*) that strengthen selection on males to identify and prefer superior partners and selection on females to signal temporal and individual differences in fecundity. Strong selection on females to maximize the growth and survival of their offspring may also generate selection pressures for mating with genetically compatible partners which, in some cases, may favor mating with multiple males (*62*).

There may also be qualitative differences in the costs of reproductive competition and secondary sexual characters to the two sexes. Although male competition and the evolution of increased body size in males is commonly associated with higher juvenile mortality and reduced longevity in males compared to females (*9*), there is little evidence that sex differences in survival are reversed in species where reproductive competition is more intense and secondary sexual characters are more highly developed in females. One possibility is that the costs of female expenditure on competition or ornamentation depress fecundity or parental investment and that these effects constrain the development of secondary sexual characters below the level at which they have measurable costs to female survival (*33*). For example, where increased competitive success in females is associated with elevated testosterone levels, these may have adverse effects on the fecundity of females (*63*) or on the development of their offspring (*64*), which constrain the evolution of further increases.

Contrasts in the operation of sexual selection in the two sexes raise the question of whether adaptations to intrasexual competition in females should be regarded as products of sexual selection. In the *Descent of Man*, Darwin commonly describes sexual selection as a process operating through intrasexual competition to breed, though where he discusses its operation in males, he describes it as operating through competition for mates. Sexual selection is now commonly defined as a process operating through intrasexual competition for mates or mating opportunities, with the result that selection pressures arising from intrasexual competition between females to conceive or rear young are generally excluded and sexual selection is, by definition, a process that is largely confined to males. An unfortunate consequence of this is that characteristics that increase the competitive ability of individuals are likely to be attributed to sexual selection if they occur in males—but not if they occur in females. As a result, it may be helpful to return to a broader definition of sexual selection as a process operating through intrasexual competition for reproductive opportunities, providing a conceptual framework that is capable of incorporating the processes leading to the evolution of secondary sexual characters in both sexes (*65*).

Conclusions

Three main conclusions should be drawn from this review. First, the theory of sexual selection still provides a robust framework that explains much of the variation in the development of secondary sexual characters in males, although the mechanisms controlling the relative intensity of reproductive competition and the relative development of secondary sexual characters in the two sexes are more complex than was originally supposed. The recognition of these complexities helps to refine the assumptions and predictions of the theory of sexual selection but does not undermine its basic structure.

Second, sexual selection operating both through intrasexual competition for breeding opportunities and through male mating preferences is common in females and can lead to the evolution of pronounced secondary sexual characters in females, as well as in males, though there are important differences in the form and costs of intrasexual competition between the two sexes. Consequently, satisfactory explanations of the evolution of sex differences requires an understanding of the operation of sexual selection in females as well as in males.

Finally, many important questions about the operation of sexual selection in females and the evolution of sex differences have yet to be answered. Where females compete directly with each other, it is often unclear precisely what they are competing for. Where females have developed obvious secondary sexual characters, it is often uncertain whether these are used principally to attract males or in intrasexual competition for resources, and how their development is limited is unknown (*33*, *49*). And, where males show consistent mating preferences for particular categories of females, we do not yet know whether they are usually selecting for heritable differences in female quality or for nonheritable variation in fecundity or for both. There is still much to be done.

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