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Social competition and selection in males and females

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During the latter half of the last century, evidence of reproductive competition between males and male selection by females led to the development of a stereotypical view of sex differences that characterized males as competitive and aggressive, and females as passive and choosy, which is currently being revised. Here, we compare social competition and its consequences for selection in males and females and argue that similar selection processes operate in both sexes and that contrasts between the sexes are quantitative rather than qualitative. We suggest that classifications of selection based on distinction between the form of competition or the components of fitness that are involved introduce unnecessary complexities and that the most useful approach in understanding the evolution and distribution of differences and similarities between the sexes is to compare the operation of selection in males and females in different reproductive systems.

1. Introduction

Although individuals of both sexes are solitary in some species, members of one or both sexes form temporary or permanent groups in many other species [1,2]. By concentrating individuals in time and space, sociality intensifies competition between them for the resources necessary for survival and reproduction, often increasing the capacity of powerful individuals to obtain a disproportionate share and strengthening selection pressures favouring traits that enhance the success of individuals in competitive encounters [3–5]. While similar processes occur in many social animals, they have been more extensively investigated in mammals than in other animal groups and we draw extensively (but not exclusively) on mammalian examples, though the conclusions that we draw are intended to be general.

Early empirical studies of social competition and its consequences focused principally on males. Their results demonstrated that, by concentrating breeding females, sociality enhanced the ability of individual males to monopolize breeding access to multiple females, favouring the development of polygyny, increasing competition between males for access to female groups and individual females and strengthening selection for male characteristics that confer success in fights or attract potential mating partners [3,6–8]. Comparative studies demonstrated that there were consistent relationships between the size of female groups and the development of secondary sexual characters in males, including increases in relative body size, the size and elaboration of male weaponry (such as male horns and canine teeth) and the extent of male ornaments [9–11].

For a combination of conceptual and practical reasons, few early studies of vertebrates initially explored the causes and consequences of social competition between females. In most groups of animals, the frequency and intensity of aggression is lower in females than in males and secondary sexual characters are generally less developed [12], with the result that their distribution and evolution has attracted less attention than comparable traits in males. In addition, in many polygynous animals, females are harder to recognize individually than males, partly because there are usually large numbers of females within social groups, and partly because they do not exhibit obvious scars as often as males do. Finally, while individual differences in access to reproduction were

immediately obvious in males as a result of their differential ability to monopolize groups of females, in species where females breed annually and have relatively long lifespans, the magnitude of individual differences in female fitness is not obvious unless the breeding success of recognizable animals has been monitored over several seasons [13,14]. Most early studies of polygynous vertebrates lacked information of this kind and as a result, did not initially appreciate the extent of individual differences in breeding success among females or their causes.

As field studies developed, the prevalence and intensity of competition between females and the magnitude of individual differences in breeding success among females became clear [4,15–17]. In particular, field studies of social mammals, including rodents [18,19], ungulates [20], carnivores [21,22] and primates [23–26], showed that, where multiple breeding females live in stable groups, reproductive competition between them is often intense and that individual differences in competitive success are often associated with substantial differences in the lifetime reproductive output of females which, in some cases, approach or even exceed those in males [27,28]. It also became clear that, as in males, contrasts in the intensity of competition between females and the development of associated traits reflect variation in social organization and mating systems. Early studies of birds recognized that the evolution of bright plumage in both sexes occurred in species where both females and males were involved in aggressive or territorial displays [17,29] and that greater development of ornamentation in females than males occurs in some species with polyandrous mating systems [7,8,30]. Studies of primate societies further showed that there were consistent relationships between the development of female weaponry and female ornaments, the form and intensity of reproductive competition between females and the structure of social groups [31,32]. The extensive influence of contrasts in social organization and social competition on the evolution of weaponry and ornamentation in both sexes was recognized in important reviews by West-Eberhard [4,17], which emphasized the fundamental similarities in the evolutionary processes operating in males and females and drew attention to parallels between the effects of intrasexual competition and those of competition between juveniles.

More recently, field studies of socially monogamous birds have produced evidence of the importance of competitive displays and mutual mate choice in species where both sexes are ornamented or brightly coloured [33,34]. In addition, studies of cooperative mammals, where young produced by a single breeding female in each group are reared by other group members, have shown that individual differences in breeding success among females are often as large or larger than in males and are associated with intense competition between females for reproductive opportunities [28,35–37]. Finally, research on a variety of animals (including insects, fish and birds) has shown that sex differences in the extent of competition for breeding commonly vary between and within populations in relation to the relative abundance of breeding partners [38–40].

One result of increasing recognition of the extent of social competition between females and its evolutionary consequences has been that the dichotomous characterization of males as competitive and aggressive and females as pacific and choosy has been replaced by the realization that reproductive competition and mate choice (and characteristics associated

with them) are widespread in both sexes [41]. Over the past decade, this has increased recognition of the qualitative similarities between the evolutionary processes operating in both sexes and led to a re-evaluation of the operation of sexual selection in males and females [34,42–49]. More recently, it has led to suggestions that it may be useful to distinguish between selection operating through ecological and social competition and to categorize selection pressures according to the different forms of social competition that are involved [4,17,34,45].

In §2, we describe four different forms of social competition that are common in both male and female vertebrates (competitive displays, fighting, competition for social rank and the suppression of reproduction by rivals) and explore their consequences for the evolution of social adaptations and secondary sexual traits in both sexes. Subsequently, we compare the relationship between social competition and selection in the two sexes. Finally, we review the problems associated with attempts to classify different forms of selection and suggest that the most useful approach may be to recognize that natural selection is a single process that operates in diverse ways through multiple components of fitness in both sexes.

2. Social competition in males and females

(a) Displays and ornaments

Competitive male displays are widespread in social animals and are used both to attract breeding partners and to repel rivals [6,50]. Visual, vocal and olfactory displays are often combined and frequently reflect the signaller's hormonal status, condition and physical strength [51–53]. For example, in ring-tailed lemurs, the scent marks of males provide information about the age, condition, status, androgen levels and relatedness of individuals [54,55]. Similarly, in baboons, the loud calls of males reflect their age, rank and physical condition [52,56]. Male displays frequently emphasize male weaponry (including teeth, horns and antlers) as well as male ornaments (including bright or elaborate plumage and pelage) [4,6,34]. While male ornamentation has evolved in some monogamous species, it is more highly developed in species with polygynous breeding systems, and especially in those where multiple males display simultaneously to females [6,57,58]. Especially in seasonal breeders, the frequency of male displays can be high, and in some species, displaying males cease feeding altogether with the result that they are unable to sustain continual reproductive activity for more than a few weeks [57,59].

Like males, females use a combination of visual, vocal and olfactory displays and the frequency and quality of displays signal their age, size and condition [4,17,34,43]. Where both sexes contribute to the defence of breeding territories, female displays are sometimes directed principally at rivals, but in many species, they are also used to attract potential breeding partners and reflect the signaller's fecundity. For example, in some cercopithecine primates, the facial colouration of females is brighter, as in rhesus macaques [60], while in several baboon and macaque species, the structure of copulatory calls given by females changes with the female's stage of oestrus [61,62]. Playback experiments show that males discriminate between calls given by females at different stages of their cycle and are most attracted to the calls of females in late oestrus [62].

Reproductive competition between females breeding in groups can also lead to the development of prominent female ornaments, especially in societies where females compete to

attract males and gain direct fitness benefits by breeding with multiple partners [43]. For example, female ornamentation is highly developed in a number of fish and shorebirds where males are primarily responsible for parental care and females compete for access to breeding partners [63,64]. Among socially monogamous birds, female ornamentation appears to be more frequent and more highly developed in species where breeding pairs form groups or colonies than in species where pairs defend separate territories [17,65].

A similar association between group-living and female ornamentation may occur in mammals. One of the most striking examples of female ornamentation are the cyclical perineal swellings found in primate species where females live in groups that include multiple breeding males and commonly mate with multiple partners [31,66]. In these species, females may increase their fitness by attracting and mating with multiple males either because this increases their fecundity directly if they increase their chance of conceiving or obtain better genes for their offspring, or through the social support that they or their offspring receive from males who have mated with them [66–70]. The size of a female's swelling increases as she approaches ovulation [71–74] and large swellings attract males [68,72,73]. In addition, some studies of baboons have found that individual differences in the size of female swellings are correlated with individual differences in fecundity and have suggested that swellings may have originated as a signal of receptivity and subsequently evolved to signal differences in individual quality [68,69]. Whatever the precise mechanism responsible for the evolution of swellings, their elaboration suggests that they are a consequence of competitive signalling that affects the access of females to limited resources that have an important influence on their fitness [69]. Since female cycles are seldom closely synchronized in these species and it seems unlikely that access to sperm limits female reproduction and the most likely explanation is that females compete to attract males in order to increase investment by males in protecting them or their offspring [67].

While both prolonged competitive displays and elaborate ornaments can be highly developed among females, they are not found in all species where reproductive competition between females is intense. For example, neither elaborate visual displays nor elaborate ornaments are obvious in singular cooperative breeders where reproductive skew among females is unusually large, and competition between females is intense [28,36]. However, little is known of the olfactory displays of females in these species and it may be the case that these are highly developed and play a similar role to the visual displays of female primates or birds. Finally, where female ornaments, like the perineal swellings, or copulatory calls produced by female primates signal cyclical changes in fertility, the costs of their production and maintenance often occur at different times from the principal costs of reproduction, with the result that their fitness costs may be low.

(b) Fighting and weaponry

Escalated fights between individuals of the same sex occur in both sexes, although their frequency varies (figure 1). Field studies of polygynous species have shown that aggression among males is often frequent and can lead to sustained physical fights, lasting until the defeat of a rival, accompanied by severe, sometimes fatal, wounding [75,76]. Fighting among

males typically peaks during periods of reproduction and commonly involves conflicts over access to females, though fights also occur over access to territories, resources and social rank and fighting success affects multiple components of male fitness [13,77]. Where males compete independently, differences in age, size, weight and stamina between contestants commonly play an important role in determining outcomes [75,78]. Fighting and other forms of reproductive competition between males are particularly frequent in seasonal breeders with polygynous mating systems where individual males can monopolize access to multiple females, as in many of the ungulates [59,75] and seals [79].

Fighting is also common between females [43,46,49] (figure 1). In many solitary species, as well as in monogamous ones, females can be as aggressive as males in territorial disputes, and as in males fighting can lead to serious injuries or even death. For example, in owl monkeys, both females and males fight to evict intruders of the same sex, wounding is common and losing can have fatal consequences in both sexes [80]. Similarly, in singular cooperative breeders, like naked mole-rats and meerkats, breeding females are usually intolerant of each other and the death of a dominant breeder is often followed by repeated and protracted fighting between individuals competing for her position [28,37]. Fighting between females is also common in many plural breeders and peaks during the reproductive season [81–83], and here, too, can lead to wounding or death [28,84]. As in males, intraspecific variation in female aggression is often associated with increased levels of testosterone, though this is not so in all species [85–87].

While it is a mistake to characterize females as pacific and competition between them for resources or mating partners is not uncommon [88,89], in most species, escalated fights between females are less frequent and are shorter than fights involving males and serious wounding is not as common [44,76,83]. There are several reasons why physical attacks may be less frequent and less intense in females than males. In some polygynous species, the immediate fitness gains (in the form of extra mating opportunities) that males can achieve as the result of a successful fight may often be greater than the potential benefits of winning fights to females [8,90]. However, where females fight for breeding status and the breeding lifespans of females are longer than those of males, the outcome of fights may have longer lasting effects on breeding success in females than males, and sex differences in the lifetime reproductive benefits of winning fights are likely to be smaller than sex differences in immediate reproductive benefits [28]. In addition, the cumulative costs associated with escalated fights may often be higher for females than for males, as they may incur fatal injuries that affect the survival of dependent offspring: for example, territorial fights among females frequently result in infant deaths in ring-tailed lemurs [91]. Finally, where females are philopatric (as in many mammals), females may be able to control the development or the presence of potential rivals, so that escalated conflicts between individuals of approximately equal physical strength are less common than in males [42].

The larger benefits of winning fights in males have commonly led to the greater development of secondary sexual characters in males in many polygynous species. In many polygynous and promiscuous mammals, males are larger than females and have more highly developed weapons [9,10,92]. While the relative intensity of social competition between males often exerts an important influence on the



Figure 1. Modes of reproductive competition in males and females. Fights among males are frequent and severe in many polygynous species, as in chacma baboons (*Papio ursinus*, (a), picture credit: Elise Huchard) but also occur among females, as in meerkats (*Suricata suricatta*, (b), picture credit: Andrew Young). Male infanticide is common in many mammals, including many polygynous primates, such as chacma baboons ((c), picture credit: Ryne A. Palombit), whereas female infanticide is also common in other species, including meerkats ((d), picture credit: Andrew Young). (Online version in colour.)

evolution of sexual dimorphism, variation in the intensity of social competition between females also plays an important role. As might be expected, sexual dimorphism in body size is often reduced in species where reproductive competition between females is intense and is reversed in some species, including some fish where males are responsible for parental care, several polyandrous shorebirds and a number of social mammals [6,42,44,93]. There is also evidence that increased reproductive competition between females can be associated with increased development of weaponry in females. For example, in monogamous primates where females defend feeding territories against neighbours, females have (relatively) larger canines than in species where females seldom contribute to territorial defence [32,94]. Similarly, in some polyandrous shorebirds where males are responsible for parental care and females compete intensely for breeding partners, females show greater development of wing spurs used in intrasexual fights [95] (figure 2).

Although there are examples where weaponry is more highly developed in females than in males, these are rare, even among species where reproductive competition is more intense among females than among males (see review by Young & Bennett [96]). The lower frequency and duration of fights between females (see above) may help to explain why this is the case. In addition, in some cases, the costs of developing or maintaining weaponry may be greater in females than in males. Alternatively, the form of intrasexual fights can differ between the sexes, favouring the development of different

characteristics in males and females [46,49] or selection for the development of weapons in females may be reinforced by their use in the defence of offspring against predators or conspecifics [97]. Finally, intense intrasexual competition between females may sometimes favour sexual mimicry rather than dimorphism. For example, in some plural breeders where female competition is intense, females show heightened testosterone levels at particular stages of the breeding cycle [86,98] and their genitalia show signs of masculinization [99–102]. Though masculinization of female genitalia may sometimes be a non-adaptive by-product of elevated testosterone levels or of increased sensitivity to androgens [103,104], sexual mimicry may also allow females to deflect aggression directed at them by dominant females or males or to control the identity of mating partners [105–107].

(c) Dominance and reproductive success

Where individuals live in stable groups, they are often able to identify each other and avoid escalated fights with individuals that have recently beaten them, so that dominance hierarchies develop [31,108,109]. Many early studies of vertebrates (and of mammals in particular) focused on species where breeding groups included multiple breeding males, including studies of wild sheep [108], deer [110], baboons [111,112], gorillas [113] and chimpanzees [114,115] and documented regular dominance relationships among males. In some species, male dominance and success in fights are

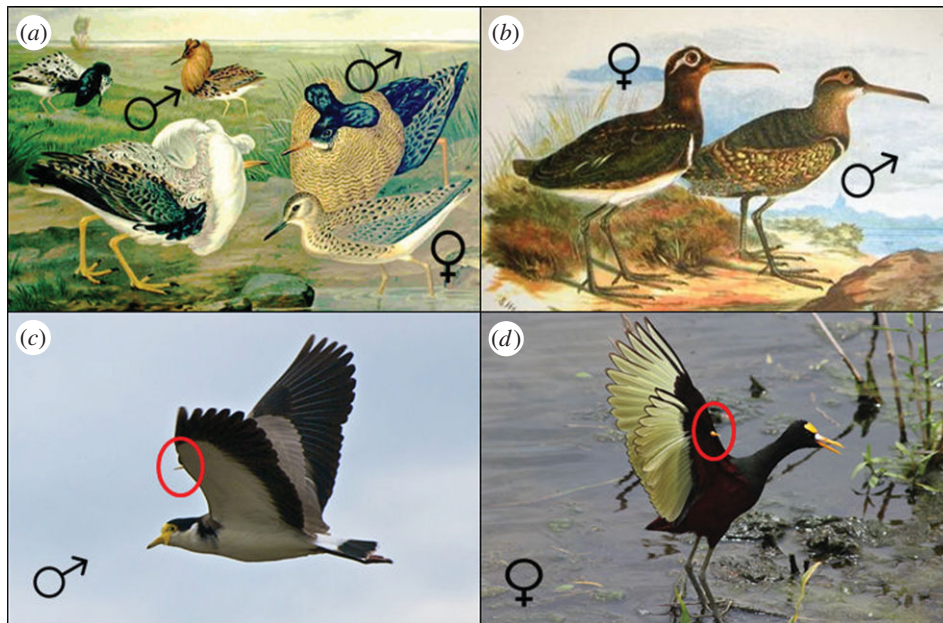


Figure 2. Ornaments and armaments in shorebirds. Males are more highly ornamented in many polygynous shorebirds where they compete with each other on leks in order to gain sexual access to females, as in ruffs (*Philomachus pugnax*, (a), illustration of a lek by Johann Friedrich Naumann), whereas females are more highly ornamented than males in some polyandrous species where they compete with each other to gain access to paternal care, as in the painted snipe (*Rostratula benghalensis*, (b), illustration by S. Herbert). Similarly, armaments (here wing spurs highlighted by circles) are more developed in males than in females in polygynous species, as in the masked lapwing (*Vanellus miles*, (c), picture credit: Gary Stockton/CC BY-NC-ND 2.0) but are more highly developed in females in some polyandrous species, as in the northern jacana (*Jacana spinosa*, (d), picture credit: Benjamin Keen/CC-BY-SA-3.0). (Online version in colour.)

effectively inseparable: for example, in red deer, bighorn sheep, elephants and many social primates, the social rank of males depends on their fighting ability, and losers suffer an immediate change in status relative to the winner and may be evicted from breeding groups [59,116–120].

Where male dominance rank depends on fighting success, the rank of males is often associated with their age, size and weight [78,79,116,121]. For example, in sexually dimorphic ungulates, where fights between males involve pushing or ramming contests, the outcome of fights often depends on the relative size and weight of contestants [27,59,118]. However, male size is not always important and its influence on dominance status depends on fighting techniques. For example, in horses, where individuals fight by biting their rivals, dominance is unrelated to body size [122]. Similarly, in social primates where males form coalitions to compete for status or access to females, the rank and social connections of allies have a more important influence on the rank and breeding success of males than their body size or condition [123–125]. For example, in Assamese macaques, the breeding success of males that have dispersing from their natal group is correlated with the strength and number of their social bonds with other males [126].

Male dominance rank is often positively correlated with access to receptive females and with mating frequency [112,116,127–130], though the strength of correlations between rank and mating success and the extent of reproductive skew among males varies widely as a result of female reproductive synchrony and female mating preferences [116,130–132]. In addition, high rank often affects access to resources as well as to alliance partners [117,121,133] and is frequently associated with benefits to health and survival [134–136]. However, high-ranking males are commonly involved in more frequent exchanges of aggression than low-ranking individuals and are more likely to be wounded [76,83] so that there are likely to be trade-offs between the relative status of males and the period for which they maintain their rank [116].

Dominance hierarchies are also common among females, though they do not occur in all species and the frequency, regularity of outcome and linearity of hierarchies vary widely between and within species [42,137,138]. As in males, rank is often established through physical contests [28,42,139] and is frequently associated with age, body size or mass [140–142]. In plural breeders where females are philopatric, adult females frequently support their daughters and other members of their group and these interventions help to establish the eventual rank and breeding success of juveniles [21,143–145]. Although females commonly support close matrilineal relatives [146–148], they can also form social bonds with unrelated individuals which may also affect their social rank [23,24,149–151].

As in males, dominance rank in females is usually positively correlated with reproductive success as well as with access to resources, though relationships vary widely in strength and have not been found in all studies [42,49,129,130,152,153]. For example, in several cercopithecine primates, high-ranking females breed earlier and more frequently, their offspring grow faster and are more likely to survive and breed successfully than those of subordinate females [153–161]. Similarly in spotted hyenas, high-ranking females have priority of access at kills, breed at younger ages, wean their offspring more rapidly, breed more frequently and produce more surviving offspring than subordinate females [21,162,163]. In some social primates, high-ranking females and their offspring are also less likely to be evicted from social groups [153], and like dominant males, show improved health and survival [135,136].

While the determinants and consequences of rank are similar in the two sexes, the strength of relationships between fighting ability, rank and reproductive success often appears to differ. Although direct comparisons of the effects of rank on fitness in males and females are scarce, the effects of fighting ability and physical strength often appear to be stronger in males than in females, where rank often depends to a greater extent on social

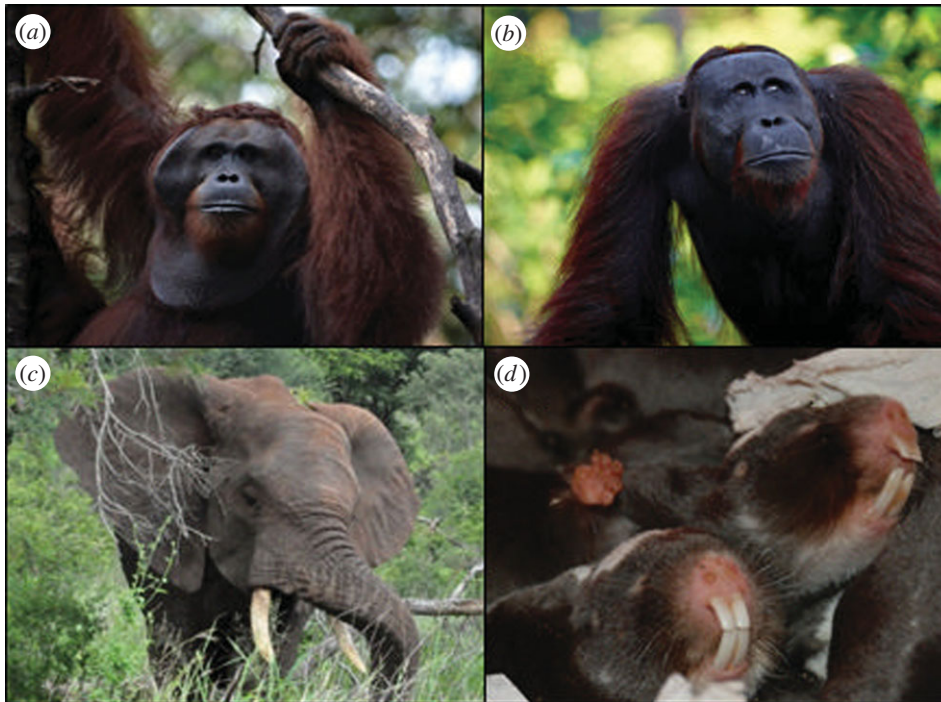


Figure 3. Physiological suppression of reproductive function in males and females. The physiological suppression of reproductive function is common among males, even in species where males are solitary, as in orangutans (*Pongo pygmaeus*), where large males with pronounced secondary sexual characters ((a), picture credit: Michael Malherbe) suppress the development and reproductive function of younger males ((b), picture credit: Michael Malherbe) living in overlapping homeranges or in elephants (*Loxodonta africana*, (c), picture credit: Elise Huchard). Reproductive suppression is also common among females in singular breeders like Damaraland mole-rats (*Fukomys damarensis*, (d), picture credit: Markus Zoetl). (Online version in colour.)

bonds and coalitionary support [25,148–150,164,165]. Rank dependency on social support may be particularly pronounced among members of the philopatric sex but can also occur in the dispersing sex [122,126]. Dominance rank in females tends to be more stable than among males: female rank is often established early in life and persists through old age [166,167], whereas the rank of males commonly changes throughout their life and the period over which individuals hold high ranks is often short [112,116,168]. The contrast in the stability of rank in the two sexes may be related to the stronger effects of kin support in females as well as to the greater intensity of reproductive competition and the greater costs of maintaining high social status in males [28].

Since no direct comparisons of the effects of social rank on the reproductive success of individuals of both sexes and on the fitness of their progeny are yet available, it is not yet possible to come to any firm conclusion concerning the relative intensity of selection on traits associated with social rank in the two sexes. It is commonly suggested that the reproductive benefits of dominance are greater in males than in females [129,130], and this may generally be the case, with the possible exception of polyandrous species and singular, cooperative breeders [35]. However, recent studies suggest that sex differences in the effects of social status on fitness are likely to vary and may often be smaller than has generally been assumed as a result of sex differences in the duration of breeding lifespans [42,49].

(d) Reproductive suppression

In addition to enhancing their social rank and reproductive success by winning physical contests and rising in the social hierarchy, both males and females can also enhance their own reproductive success by evicting rivals or suppressing

their reproductive attempts (figure 3). In many species, adult males also evict adolescents of the same sex [169–173] who often show heightened mortality levels before they are integrated into a new breeding group [174]. Where dominant males tolerate the presence of younger individuals, aggression directed at younger males, or in some cases, the presence of older and more dominant males, can affect the hormonal status of younger males and retard or depress their sexual behaviour. For example, in African elephants, interactions with older dominant males can ‘switch off’ reproductive activity (‘musth’) in younger males [119,175]. Interactions between males can also delay the development of subordinates, with the result that subordinates often show reduced body mass, condition and gonad size, less active scent glands, reduced development of secondary sexual traits, decreased levels of reproductive and growth hormones and lower frequencies of sexual behaviour [176–179]. Eviction or reproductive suppression among males is particularly prevalent in systems where dominant males cannot guard receptive females effectively or where scramble competition for breeding opportunities is important. In addition, reproductive suppression may benefit dominant males by ensuring that subordinate males are less attractive to females [180] or suffer disadvantages in sperm competition [181] as well as by reducing the costs of maintaining dominance and of mate-guarding to alpha males.

In some mammalian species, males kill unrelated dependent juveniles and this provides them with additional mating opportunities by allowing them to impregnate the victim’s mother, who typically resumes to oestrus within a few weeks after losing a dependent offspring [182,183]. Infanticide often involves males that have recently immigrated into social groups, but also occurs in societies where several males are associated with groups of females [184]. Male infanticide is most frequent where male tenure is short,

females have a long lactational infertility and infanticidal males can gain sexual access to the mother of the killed infant [185,186]. By contrast, it is unusual where females conceive immediately after giving birth (as in equids, some terrestrial carnivores and many seals). Some observations suggest that males may preferentially target future rivals: for example, males appear to kill male offspring more often than female offspring in chimpanzees but the generality of this trend and the reasons for it are not yet clear [187,188].

While adult males are frequently intolerant of each other's presence, they can be more tolerant of the presence of kin than non-kin. For example, in multi-male coterries of prairie dogs, relationships between resident males are more amicable and less competitive when males are close kin than when they are unrelated [78]. Similarly, in alpine marmots, dominant males are more aggressive with unrelated subordinates, and suppress their development to a greater extent than that of related subordinates [189]. In chimpanzees, too, maternally related males are more likely to affiliate with and support each other than the offspring of unrelated females, although not all allies are related [190]. However, kinship appears to affect some forms of cooperation more than others. For example, while male chimpanzees selectively support related males in competitive encounters with other males, there is no evidence of kin-bias in hunting behaviour and males are no more likely to share meat with maternal kin than with unrelated males [191].

Females adopt many of the same tactics to suppress development and reproduction by rivals. In singular breeders, dominant females commonly evict subordinates from the group when they reach adolescence, approach adult size or attempt to breed [28,192]. Suppression of reproductive function in subordinates is at least as common among females as among males. In many singular breeders, dominant females direct regular aggression at older adolescents which can reduce levels of reproductive hormones and delay their development [179]. In some plural breeders, too, dominant females direct frequent aggression at subordinates which delays their development, disrupts their reproductive cycles and causes them to down-regulate their reproductive systems or abort litters [179,193]. For example, in yellow baboons, dominant females direct frequent aggression at subordinate females during the follicular phase of their cycles, raising the number of cycles before they conceive [26]. Aggression directed at females shortly after mating can reduce implantation success and induce abortion [42,194,195].

Like males, females are often more tolerant of individuals of the same sex if they are close relatives than if they are more distant relatives or unrelated. In some voles, females preferentially settle close to relatives and those with ranges abutting those of relatives breed at younger ages, rear more offspring and have higher rates of survival to the next breeding season than those with ranges abutting those of unrelated individuals [196,197]. Similarly, in meerkats, the probability that a dominant female will evict a subordinate increase as her coefficient of relatedness to the dominant female falls [198]. In some cases, the suppression of subordinate development and reproduction eases where group size is low or food availability is high, suggesting that dominant females adjust their behaviour to the availability of resources [35,198].

Infanticide by females is also widespread in many social species and is probably more frequent than infanticide by males [199,200]. For example, in black-tailed prairie dogs,

females commonly kill the offspring of subordinates occupying neighbouring burrows, even if they are close relatives [78]. Like males, females may preferentially target their future rivals. For example, in some cercopithecine monkeys, where females are philopatric and the relative rank and reproductive success of individuals depends on the rank and size of their matrilineal group, mothers direct higher rates of aggression at the daughters of subordinate females than at their sons [201], generating higher frequencies of mortality in female offspring [202,203]. While female infanticide has been extensively documented in mammals, it also occurs in other groups. For example, in some polyandrous birds, females who acquire breeding territories destroy nests or kill the dependent young of their rival and their behaviour parallels that of males in polygynous mammals [204,205].

While individuals of both sexes commonly evict rivals, sex differences in the frequency of eviction and in the intensity of overt competition between group members often appear to be greatest in whichever sex most frequently remains and breeds in their natal group. For example, in many social animals where females typically remain and breed in their natal group while males disperse, protracted conflicts over group membership are more frequent between females than between males while the reverse may be usual where males are commonly philopatric [35,206,207]. This may be partly because members of the dispersing sex are unlikely to invest heavily in competition to remain in the group, or established adults are less likely to react aggressively to natal of the dispersing sex which do not represent serious competitors because they are closely related to residents of the opposite sex who are unlikely to mate with them. In addition, increased conflict may occur between individuals of the philopatric sex because, if they do leave their own group, they are frequently prevented from joining established breeding groups and are consequently less willing to leave [206,208].

3. Social competition and selection in males and females

This brief survey emphasizes the importance and similarity of social competition in both sexes as well as its pervasive impact on selection pressures. In group-living animals, competition for resources of all kinds is mediated by social mechanisms operating within the group they live in. Although competition between males for mates and breeding territories is common, females, too, frequently compete intensely for breeding sites, reproductive opportunities, membership of breeding groups or social status within them. Social competition also occurs between groups. In many animals, members of different breeding groups compete with each other for resources or space and frequently interfere with each other's breeding attempts. Competition between groups as well as between residents and intruders exerts an important influence on the evolution of group size and dispersal patterns as a result of the pervasive tendency for larger social units to displace smaller ones [209,210]. Similarly, where both sexes are solitary, social interactions between neighbours or between residents and intruders exert an important influence on the reproductive success of individuals.

Although studies of competition most commonly focus on adults, social competition can occur at all stages of development [4,17]. In some mammals, competition between

litter-mates begins before birth and persists throughout the period of lactation and early development, affecting both the survival of neonates and juveniles and their subsequent reproductive success and longevity [162,202] and in some cases, it can lead to unusual patterns of development, such as the precocious development of teeth in spotted hyenas associated with intense sibling rivalry [211] or the striking natal coats of infants in some primates [4,17,212]. In others, social competition can lead to the development of traits that mimic the characteristics of the opposite sex, as in fossas and in spotted hyenas [42,107].

The common property in all these cases is that competing individuals belonging to the same subdivision of the population (which may be a deme, a group, a cohort or a litter) play repeated zero-sum games with each other, which involve fights over high-value resources that are seldom shared between competitors, and some individuals consistently win these contests, generating large individual differences in fitness. Where individuals engage simultaneously or successively in competitive interactions with many competitors and can monopolize a large proportion of available resources or breeding opportunities, competition is likely to be particularly intense and selection for traits that increase competitive ability is likely to be extremely strong. The effects of competitive success are seldom limited to a single component of fitness and commonly influence the growth, fecundity and survival of individuals as well as the fitness of their offspring. In addition, social competition often mediates the effects on fitness components of a wide range of environmental challenges, including starvation, disease [135,213,214] and predation [215,216]. As a result, in group-living species, it is often difficult to conceive of selection pressures that are unaffected by social competition with the result that the distinction between 'social' and 'ecological' selection proposed by West-Eberhard [4,17] and others [34,45] is impractical.

As the previous sections show, recent research emphasizes the fundamental similarity in the causes of social competition in the two sexes and emphasizes that most contrasts between the sexes are quantitative rather than qualitative, matters of degree rather than differences in kind. In both sexes, the intensity of reproductive competition is determined partly by contrasts in the number of individuals competing for breeding partners as a result of variation in the Operational Sex Ratio, generated by sex differences in the time required by individuals to recover from an attempt to reproduce ('time out' or 'dry time') [39,217,218] and by variation in the number of individuals whose sexual development is delayed or suppressed; partly by relationships between competitive success and reproductive success in the two sexes, including Bateman gradients [8,40,218]; and partly by factors affecting the ability of individuals to monopolize breeding partners and resources necessary for reproduction [7,43,210,219].

The extent of sex differences in behaviour and competition and in the selection pressures these generate is in the process of being re-validated in the light of more precise and more extensive data from natural populations. For example, while it has been widely accepted that investment in competitive displays, in fighting and in competition for dominance status is often greater in males than in females, aggressive competition is also frequent among females and can be more intense than among males [46,49]. We still know relatively little about the effects of variation in competitive success on fitness in the two sexes or about trade-offs

between the capacity of individuals to monopolize breeding opportunities at particular stages of the lifespan and the duration of effective breeding, which often contributes a substantial proportion of variation in lifetime reproductive success [16,116]. For example, no study of a social vertebrate has yet been able to make a direct comparison of relative effects of social rank on peak breeding success, on the duration of successful breeding and on lifetime reproductive success in both sexes.

The consistency of sex differences in social competition is also being re-evaluated. Several recent studies have shown that sex differences in reproductive competition differ between populations as well as within the same population over time [38,40,43,116] but we know little of the extent or the distribution of these differences. Similarly, while it is widely accepted that mating preferences are usually more highly developed in females than males and individual variation in attractiveness is commonly a more important cause of variation in fitness in males than in females [6,220], there is increasing evidence that the strength of female mating preferences varies between and within species [221,222] and that males, too, often show consistent mating preferences [223,224] that can lead to the evolution of conspicuous ornaments in females [33,65,66,225].

Finally, sex differences in the extent of individual differences in breeding success and in the potential strength of selection pressures are being re-assessed. While it is generally assumed that in polygynous and promiscuous species individual differences in the potential pay-offs of successful competition are larger in males than females, the shorter breeding lifespans of males in these species combined with the consistency of individual differences in breeding success among females mean that sex differences in the extent to which lifetime breeding success differs between individuals may often be relatively small [16,49] and can be reversed in species where alloparental care alleviates the costs of maternal investment [28,35,36]. Moreover, transgenerational maternal effects on offspring phenotypes [226–228] may result in a greater covariance between maternal and offspring fitness than between paternal and offspring fitness and further attenuate contrasts in variance in reproductive success between the sexes after several generations [49].

4. Categories of selection

The underlying similarity in the operation of selection in males and females has recently generated discussion of the distinction between natural selection and sexual selection [34,43–46,48,49,229–232]. Darwin developed the theory of sexual selection to account for the evolution of secondary sexual characters and was well aware that they occur in both sexes. Although the *Descent of Man* focuses primarily on the evolution of secondary sexual traits in males as a result of mating competition, he appreciated that both of the two forms of sexual selection that he described (intra-sexual competition to breed and intersexual mate choice) can occur in both sexes and can lead to the evolution of secondary sexual characters. For example, in the General Summary of the *Descent of Man*, he describes the operation of sexual selection in more general terms than he uses in chapters where he focuses on the evolution of secondary sexual characters in males: '*Sexual selection depends on the*

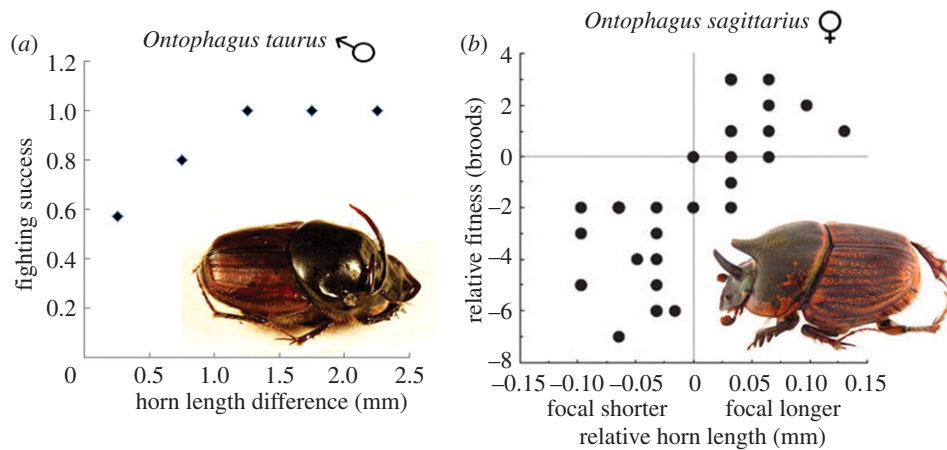


Figure 4. Horn length and fighting success in male and female *Onthophagus* beetles. (a) Relationship between male fighting success and horn length in *Onthophagus taurus* ($n = 27$ contests). Graph adapted from Moczek & Emlen [235], fig. 3. Picture credit: Tom Murray. (b) Relationship between relative horn length and relative fitness of competing females in *O. sagittarius*. Positive values on the x - and y -axes represent cases where, in pairs of competing females matched for body size, the focal female had a larger horn and produced more broods relative to her competitor. Graph reproduced from Watson & Simmons [236], fig. 3. Picture credit: Udo Smidt. (Online version in colour.)

success of certain individuals over others of the same sex, in relation to the propagation of the species. The sexual struggle is of two kinds; in the one it is between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst, in the other, the struggle is likewise between the individuals of the same sex, generally the females, which no longer remain passive, but select the more agreeable partners' (our italics). However, in line with Darwin's more specific descriptions, sexual selection is now usually defined as operating exclusively through intrasexual competition for mating opportunities or through competition for access to gametes of the opposite sex [6,48,218].

While definitions of sexual selection that restrict it to selection operating through mating success offer greater precision, they have the disadvantage that they limit the effective role of sexual selection in females, where direct competition is usually over opportunities to breed or resources necessary for reproduction (including paternal investment) rather than over access to males or to sperm [46,49]. As a result, most examples of selection operating through social competition between females, including selection favouring female ornaments or weapons that allow individuals to compete successfully for nuptial gifts or male investment in offspring [233,234], would be excluded and the evolution of traits serving similar functions in males and females would have to be attributed to different evolutionary processes.

Perhaps the example that crystallizes this dilemma most clearly is a study of *Onthophagus* dung beetles where both sexes have evolved large horns that are used in contests over access to dung that is used to form balls where eggs are laid (figure 4). Competition for dung leads to selection operating through individual differences in mating success in males and through individual differences in fecundity in females, and for this reason, advocates of a narrow definition of sexual selection regard horns in males as a product of sexual selection but attribute their evolution in females to other evolutionary processes, such as social selection [34]. While it is certainly possible to draw this distinction, it is difficult to avoid thinking that future generations of evolutionary biologists will be puzzled to find that similar traits in males and females, generated by identical forms of competition for the same resource are attributed to different evolutionary processes.

One possible solution to the semantic problem raised by these comparisons is to use sexual selection to refer to all selection pressures that are influenced by the sex of individuals [49,229,237]. However, this has the disadvantage that, in sexual organisms, few (if any) selection pressures are unaffected by the sex of individuals. Alternatively, sexual selection might be used either to refer to all selection pressures operating through intrasexual competition to breed (rather than to mate) or to all selection pressures favouring the evolution of secondary sexual characters [43,44]. This, however, would include selection operating through female competition for resources and would introduce the difficulty of distinguishing reproductive competition from competition for resources necessary for survival [43,48].

Recently, two reviews have advocated using the framework proposed by West-Eberhard in 1983, involving an initial division of selection pressures into social selection (those operating through all forms of social competition) and selection pressures operating through other forms of competition, as well as a secondary division of social selection into selection pressures operating through competition for mating opportunities (sexual social selection) and those operating through all other forms of social competition (non-sexual social selection) [34,45]. For enthusiasts, they also offer the possibility of further subdivisions, including mutual sexual selection, mutual social selection, individual social selection and indirect social selection [34].

While it is useful to recognize the diversity of ways in which social competition can operate, this approach, too, introduces unnecessary complexities and has substantial disadvantages [230]. In group-living species, social competition affects all selection pressures so that it is unclear what social selection excludes. Moreover, as successful social competition commonly affects multiple components of fitness in both sexes, there are practical difficulties in attributing the evolutionary processes responsible for particular traits to sexual social selection versus non-sexual social selection: for example, should male traits that increase competitive success (like large body size or large canines) be regarded as products of sexual social selection (because they affect mating success) or as products of non-sexual social selection (because they affect survival)? Finally, even if it was possible to distinguish clearly

between sexual social selection and non-sexual social selection, similar adaptations to reproductive competition in males and females (like the horns of *Onthophagus* beetles) would still be attributed to different evolutionary processes, extending an unnecessary and stereotypical distinction between the evolutionary processes operating in the two sexes.

The difficulties of attempting to distinguish between ecological, social and sexual selection should raise questions about the need to categorize different forms of natural selection and the desirability of doing so. It is now widely recognized that sexual selection is a sub-category of natural selection rather than an alternative process. Recent studies of sexual organisms have shown how selection operates on males and females through many components of fitness at many stages of their lifespans; how it can be driven by competition with different types of competitors for different resources at different stages of the breeding cycle; how its operation varies in strength, direction and consistency and how it can have many different outcomes and consequences. While it can be useful to identify different forms of competition and contrasting types of selection, natural selection is a single

process that operates in diverse ways [238]. Contrasts between different types or forms of natural selection are artificial and even the most elaborate classifications of selection pressures are likely to obscure important differences and disguise important similarities, as the recent history of research on sexual selection shows. There is little evidence that selection operating through different forms of social competition has qualitatively different outcomes so, to extend our understanding of the evolution of differences between the sexes, it may be more useful to explore and compare the ways in which natural selection operates in males and females in contrasting systems than to prolong attempts to develop classifications of selection based on the form of competition or the components of fitness that are involved.

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