In many animals, males develop elaborate weapons or ornaments and become increasingly aggressive as they reach sexual maturity. Over 90 years before the publication of the *The Descent of Man* (Darwin 1871/1958), these ‘secondary’ marks or characters of sex were a focus of the attention of the anatomist John Hunter (1780, 1837) who distinguished them from the sex organs, which he identified as the ‘primary’ characters of males and females. Hunter realized that the development of secondary sexual characters was related to ecological differences between species.

The males of almost every class of animals are probably disposed to fight, being, as I have observed, stronger than the females; and in many of these are parts destined solely for that purpose, as the spurs of the cock, and the horns of the bull... One of the most general marks [of sex] is the superior strength of make in the male; and another circumstance, perhaps equally so, is this strength being directed to one part more than another, which part is that most immediately employed in fighting. This difference in external form is more particularly remarkable in the animals whose females are of a peaceable nature, as are the greatest number of those which feed on vegetables, and the marks to discriminate the sexes are in them very numerous. (Hunter 1837, page 45)

In the *The Descent of Man* Darwin (1871/1958) adopted Hunter’s distinction between primary and secondary sexual differences with an important difference. Instead of using secondary to refer to sexually dimorphic traits that develop some time after hatching or birth, Darwin drew a functional distinction: his primary sexual characters were those connected with the act of reproduction itself, while his secondary sexual characters were used in intrasexual competition to breed. He termed the evolutionary process generating them ‘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’ (Darwin 1871/1958, page 209). He emphasized the central importance of intrasexual competition in the evolution of secondary sexual characters and described how sexual selection can take two distinct forms (Darwin 1871/1958, page 614): ‘sexual selection depends on the 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 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 individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners’.

Subsequent developments of Darwin’s theory explained why intrasexual competition and secondary sexual characters are often more highly developed in males. Building on empirical studies of
Drosophila by Bateman (1948); Trivers (1972) argued that it is the relative expenditure by males and females on gametes plus parental care (‘parental investment’) that determines the relative intensity of competition for breeding partners in the two sexes. Sex differences in parental investment affect the time necessary to complete a successful breeding attempt, which limits the potential rate at which males and females can process partners of the opposite sex (potential reproductive rate; Clutton-Brock & Parker 1992; Ahnesjo et al. 2001) and leads to biases in the operational sex ratio (OSR: the ratio of males and females ready to breed at a particular time; Emlen & Oring 1977; Simmons 1995).

While secondary sexual characters are usually more highly developed in males than females, females show some development of secondary sexual characters (including weaponry, brightly coloured plumage or pelage and elaborate ornaments) in a substantial number of animals (Andersson 1994; Kraaijeveld et al. 2007). In some species, they possess secondary sexual characters that are absent in males and, in a few, they show greater development of traits that are present in both sexes (Clutton-Brock 2007). The presence of secondary sexual characters in females raises important questions about the evolutionary mechanisms responsible for them and for their distribution (Isaac 2005; Clutton-Brock 2007; Kraaijeveld et al. 2007). Although Darwin (1871/1958) was aware of the presence of secondary sexual characters in females, he was primarily concerned with explaining the evolution of secondary sexual characters in males, noting in passing (page 614), 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’. Almost all subsequent reviews have maintained the same bias (Huxley 1938, 1942; Ghiselin 1974; Andersson 1994). In this paper, I attempt to redress the balance by reviewing our existing knowledge of the development and distribution of secondary sexual characters in females. I first examine the processes leading to the evolution of secondary sexual characters in females, then describe their distribution across species with contrasting breeding systems, and finally compare the operation of sexual selection in the two sexes.

**REPRODUCTIVE COMPETITION BETWEEN FEMALES**

Both of the forms of sexual selection described by Darwin (see above) occur in females as well as males. In a substantial number of animals, females compete between themselves for access to breeding territories or other resources necessary for conception or rearing offspring (Floody 1983; Heinsohn & Legge 2003; Emlen & Wrege 2004; Andersson 2004, 2005). In group-living species where several mature females breed each year, females commonly compete for social rank, which is often related to their ability to produce or rear offspring (insects: Reeve 1991; birds: Vehrencamp 1977; Bertram 1992; primates: Fedigan 1983; Silk 1997; ungulates: Clutton-Brock et al. 1982; carnivores: Holekamp & Smale 2000; Clutton-Brock et al. 2001; Hofer & East 2003; Hodge et al. 2008). In some cooperative breeders, one dominant female in each group usually prevents most (and, in some cases, all) other females from breeding by a combination of physiological suppression (marmosets: French 1997; mole-rats: Faulkes & Abbott 1997; meerkats: Clutton-Brock et al. 2001) and infanticide (meerkats: Clutton-Brock et al. 1998; Young & Clutton-Brock 2006; wild dogs: Creel & Creel 2001) and eviction of potential competitors from their group (wild dogs: Malcolm & Marten 1982; Creel & Creel 2001; meerkats: Clutton-Brock et al. 1998, 2006). In most of these ‘singular’ cooperative breeders, dominant females can maintain their status for several years while, in some species where they do not forage for themselves and the extrinsic risks of mortality are low, they live substantially longer than helpers or workers (Clark & Faulkes 1997; Carey 2001; O’Connor et al. 2002; Sherman & Jarvis 2002; Damman & Burda 2005). As a result, individual differences in breeding success and the degree of reproductive skew among females can be unusually large and can exceed the variance in breeding success among males (Hauber & Lacey 2005; Clutton-Brock et al. 2006; Clutton-Brock 2007). Since only a small proportion of females can breed as dominants, competition for social status can be intense and contests between females can be lethal.

Females also commonly compete for access to mates. Female competition for mates is widespread in polyandrous birds where OSRs are biased towards females (Emlen & Oring 1977; Oring et al. 1991a, b) as well as in some insects where males produce unusually large sperm (Lorch 2003; Bjork & Pitnick 2004) and some mammals where the sperm supplies are depleted by frequent mating (Dewsbury 1982, 2005). Female competition for mating access also occurs in species where OSRs are male biased but individual differences in their ability to invest in offspring or in the number of eggs or offspring they can care for are large. For example, in the monogamous seahorse, Hippocampus subelongatus, where males brood eggs and adult sex ratios are often biased towards females, female competition is common and body size appears to exert a stronger influence on breeding success in females than in males (Kvarnemo et al. 2007). In addition, female competition for mates is common where females gain direct or indirect benefits from mating with multiple partners in the course of a single breeding cycle (Tregenza & Wedell 1998; Fisher et al. 2006). Finally, female competition for mating access is likely to occur when individual differences in the direct or indirect benefits that males can offer as mating partners are large and the most preferred male(s) cannot service all receptive partners (Gowaty 2004; Bro-Jørgensen 2007).

In many species, sex roles are flexible and the relative frequency of intrasexual competition in the two sexes varies between stages of the reproductive cycle (Gowaty 2004; Gowaty & Hubbell 2005). For example, in two-spotted gobies, Gobiusculus flavescens, the relative intensity of intrasexual competition for mating partners in the two sexes varies throughout the breeding cycle as the relative numbers of receptive females and males change (Amundsen & Forsgren 2001; Forsgren et al. 2004). Similarly, in some ungulates where OSRs are generally male biased and males compete intensely for access to females, females that are close to oestrus and need to mate rapidly compete for access to breeding males (Bebie & McElligott 2006; Bro-Jørgensen 2007). In bush crickets, Tettigonidae, where males bring nuptial gifts to receptive females, manipulation of food availability to males changes the OSR and affects the relative frequency of competition for mates in males and females (Simmons & Gwynne 1993; Simmons 1995; Kvarnemo & Simmons 1999).

The phenotypic characters that affect the ability of females to acquire breeding opportunities, high status or mates are often similar to those that affect the acquisition of mating opportunities by males in polygynous species. They include the individual’s age, weight and hormonal status, as well as the rank of her mother (insects: Reeve 1991; Reeve & Ratnieks 1993; primates: Walters & Seyfarth 1986; Silk 1987; carnivores: Holekamp et al. 1996; Engh et al. 2000; Holekamp & Smale 2000; Clutton-Brock et al. 2006). The identity of alliances and coalition partners may also be important in species where related females support each other in competitive interactions with members of other matrilines and the social rank of individuals, as well as their reproductive success, depends on the rank of their matriline (Chapais 1992; Holekamp et al. 1996). The relative rank of matrilines increases with their size and, in some species, females from dominant matrilines focus their

**MALE MATING PREFERENCES**

In many animals, males also show preferences for mating with particular individuals or categories of females which often generate competition between females to attract males (Herbert 1968; Amundsen 2000a; Kraaijeveld et al. 2007). Male mating preferences have now been documented in insects (Dewsbury 1982; Kvarnemo & Simmons 1999; Bondursiansky 2001), fish (Sargent et al. 1986; Berglund & Rosenqvist 2001, 2003; Kvarnemo et al. 2007), lizards (Lebas & Marshall 2000; Orrell & Jenssen 2002), birds (Amundsen 2000b; Jones et al. 2001; Schamel et al. 2004; Torres & Velando 2005; Kraaijeveld et al. 2007) and mammals (Herbert 1968; Bergler 1989; Keddy-Hector 1992; Muller & Thalmann 2000; Domb & Pagel 2001; Craig et al. 2002; Preston et al. 2005; Parga 2006). Like female competition for males, the relative choosiness of males varies with the availability of partners and can differ between local populations (Simmons & Gwynne 1993) and between stages of the breeding cycle (Amundsen & Forsgren 2001).

Male preferences vary. In some species, males prefer familiar partners (Huck & Banks 1979) while, in others, they prefer novel partners (Orrell & Jenssen 2002). Sometimes, males prefer older, larger or more dominant partners (Szykman et al. 2001; Werner & Lotem 2003; Wong & Jennions 2003; Herdman et al. 2004; Preston et al. 2005; Muller et al. 2006; Kvarnemo et al. 2007) while, in others, they prefer younger partners (Buss 1989; Jones 1996; Orrell & Jenssen 2002; Sugiyama 2005). In several species, males also show consistent preferences for partners that have not mated recently: for example, male Drosophila melanogaster are less likely to court inseminated than un inseminated females while male rats, Rattus norvegicus, prefer unmated oestrous females to ones that have already mated several times (Zucker & Wade 1968). In species where females are ornamented or brightly coloured, males commonly show a preference for brighter or more highly ornamented females (Berglund et al. 1997; Lebas & Marshall 2000; Amundsen & Forsgren 2001; Domb & Pagel 2001; Berglund & Rosenqvist 2003; Torres & Velando 2005; Griggo et al. 2005). In addition, like females, males sometimes copy each other’s choice of partners, reinforcing the effects of individual choice (Widemo 2006).

Male mating preferences may often serve to increase their reproductive success, as the characteristics of females that they prefer are often correlated with individual differences in fecundity or with the proximity of females to conception (McLennan 1995; Berglund et al. 1997; Jones et al. 2001; Szykman et al. 2001; Ruscio & Adkins-Regan 2003; see below). Few studies have yet investigated the additional possibility that male mate choice may also affect the quality of offspring, but a recent study of house mice, Mus domesticus, suggests that this may be the case: when males were experimentally mated with females they did not prefer, they produced offspring with lower viability and poorer performance than those allowed to mate with preferred females (Drickamer et al. 2003; Gowaty et al. 2003). Interspecific contrasts in male preferences may often be related to variation in the effects of particular female characteristics on paternity certainty, fecundity or rearing success. For example, in chimpanzees, Pan troglodytes, where males do not invest in their offspring and older females have higher breeding success than younger ones, males prefer older partners, whereas in humans, where males commonly provide resources for their offspring and paternity uncertainty has high costs, males commonly prefer younger partners (Symons 1979; Buss 1989; Jones 1996; Sugiyama 2005; Muller et al. 2006).

Where females compete for the attention of males, selection may favour the evolution of signals that indicate their fecundity and attract the attention of males. For example, in Barbary macaques, Macaca sylvanus, the mating calls of fertile and infertile females differ and calls given by fertile females are more likely both to stimulate ejaculation by their partners and to attract the attention of other males (Pfefferle et al. 2007). In humans, the voices of women become more attractive when they are fertile (Pipitone & Gallup 2008) and studies of female lap dancers show that they earn significantly more in tips from clients during their fertile periods than at other stages of the cycle (Miller et al. 2007). Selection to attract males has probably played an important role in the evolution of exaggerated female ornaments, such as the scales of emu did flies, as several recent studies have shown that their size, structure or colouring are associated either with temporal variation in fecundity or with individual differences (see next section).

**BREEDING SYSTEMS AND SECONDARY SEXUAL CHARACTERS IN FEMALES**

The association between breeding systems and the development of secondary sexual characters in males (Clutton-Brock et al. 1977; Plavcan 2004) suggests that their development in females, too, should vary between polygynous, monogamous and polyandrous species. Secondary sexual traits associated with direct intrasexual competition should be most highly developed in females of polyandrous species where OSRs are usually female biased (Trivers 1972; Emlen & Oring 1977) or where competition between females for breeding opportunities is unusually strong, as in many singular cooperative breeders (Clutton-Brock et al. 2006; Clutton-Brock 2007) and least developed in polygynous species where OSRs are biased towards males and females do not defend resources or territories. Among monogamous species, traits associated with competition for breeding opportunities should be most highly developed in females in species where females play an important role in the defence of resources or territories (West-Eberhard 1983), while female ornamentation might be expected to show the greatest development where OSRs vary throughout the reproductive cycle, where females can gain important benefits from mating with multiple partners, or where both sexes can gain substantial benefits from mate choice and males as well as females select partners on the basis of phenotypic characters. Although there has yet to be a systematic quantitative analysis of the distribution of secondary sexual characters in females, their distribution appears to be consistent with these predictions, although inconsistencies and surprises are common.

**Polyandrous Species**

In many birds with polyandrous mating systems, females typically compete more frequently or intensely for breeding opportunities than males and are sometimes the larger sex (Jenni 1974; Erickman 1981, 1983; Berglund et al. 1986; Oring et al. 1991a; Owens & Thompson 1994; Andersson 1995; Ahnesjo et al. 2001; Berglund & Rosenqvist 2003). Females are also commonly brighter, more strikingly marked or highly ornamented than males in polyandrous birds, although this is not the case in all species (Jenni 1974; Trivers 1985; Andersson 1994; Eens & Pinxten 2000; Ahnesjo et al. 2001; Houde 2001). Why females are more highly ornamented than males in some polyandrous animals but not in others is not well understood (Trail 1990): one possibility is that females are more likely to be brightly coloured where males may invest and breed with multiple partners, making multiple choices of mate during their breeding lives (Kraaijeveld 2003). In other cases, variation in female coloration may be related to sex differences in the roles of the two sexes in territory defence and in the sites at which they display. In eclectus parrots, Eclectus roratus, for example, females are bright red and blue while males are bright...
green. Incubating females are tended and provisioned by multiple males and sex differences in colouring appear to be related to the contrasting roles of the two sexes: females do not need to be cryptic and display below the canopy where their bright colouring contrasts with the dark limbs and trunks of the trees they nest in, whereas males forage in the canopy and their coloration reflects a compromise between the need for camouflage from predators while foraging and the need for conspicuous displays (Heinsohn et al. 2005).

Several studies have investigated whether females show elevated testosterone levels in polyandrous species but there is little evidence that they do so (Fivizzani & Oring 1986; Eens & Pinxten 2000; Goymann & Wingfield 2004; Voigt & Goymann 2007). However, in dunnocks, Prunella modularis, females in breeding groups that include a single male and more than one female have higher testosterone levels than those in monogamous pairs (Langmore et al. 2002). One possible reason for the absence of elevated testosterone levels in females in polyandrous species is that females may show enhanced sensitivity to testosterone rather than elevated testosterone levels. For example in African black coucals, Centropus griffii, females have a higher mRNA expression of androgen receptors than males (Voigt & Goymann 2007) and in some fish where reproductive competition between females is intense, the brain gene expression of dominant females resembles that of males (Aubin-Horth et al. 2007).

Monogamous Species

Females also show pronounced secondary sexual characters in many socially monogamous species. Where secondary sexual characters are similar but less highly developed in females than males the traditional explanation is that the presence of secondary sexual characters in females is a consequence of genetic correlations (Lande 1980; Trail 1990; Amundsen 2000a, b, c). However, while selection experiments show that selection on secondary sexual characters in males can lead to correlated responses in females (Harrison 1953; Wilkinson 1993; Price & Birch 1996; Chenoweth & Blows 2003, 2005), their effects are usually weak and comparative studies indicate that sex-linked modification of the expression of ornaments is more common than sex-linked inheritance of ornament genes (Wiens 2001; Emlen et al. 2005), suggesting that explanations of this kind are unlikely to account for the maintenance of secondary sexual characters in females. In addition, comparative studies show that evolutionary changes in female ornamentation and transitions between dimorphism and monomorphism are common (Amundsen 2000b; Kraaijeveld et al. 2007).

An alternative explanation is that in monogamous species where both sexes are brightly coloured or carry other ornaments, mutual mate choice may often play an important role in the development of secondary sexual characters in both sexes, reinforcing genetic correlations between them (Amundsen 2000a; Kraaijeveld et al. 2007). Mutual mate choice has now been demonstrated in a wide variety of species, including fruit flies, rotifers, termites, amphipods, fish, amphibians and birds (Kraaijeveld et al. 2007). Female plumage may commonly provide males with an indication of a female's fecundity or capacity for parental investment (Møller 1993; Blount et al. 2002). For example, in northern cardinals, Cardinalis cardinalis, brighter females feed nestlings more than duller ones (Linville et al. 1998) while female zebra finches, Taeniopygia guttata, that have been experimentally fed show enhanced fecundity and are preferred as mating partners over unfed females, although they are indistinguishable to the human eye (Monaghan et al. 1996).

A wide variety of ecological factors may also affect the evolution of ornamentation or other secondary sexual characters in females in monogamous species. Where both sexes have similar ornaments, females as well as males are commonly involved in aggressive displays aimed at rivals, suggesting that intrasexual competition is involved (West-Eberhard 1983; LeBas 2006). Mutual mate choice would also be expected to generate larger benefits where both sexes defend resources or contribute to parental care (Burley 1983; Kvarnemo et al. 2007). Showy signals in females may also offer larger benefits where males make repeated choices between multiple alternative partners and, as expected, the degree of ornamentation in both sexes increases with interspecific differences in annual divorce rates (Kraaijeveld 2003). Female plumage may also be affected by the risk of predation: for example, in some groups of birds, there is a negative correlation between the brightness of females (but not the brightness of males) and the frequency of nest predation (Martin & Badyaev 1996).

Cooperative Breeders

In many cooperative or eusocial vertebrates, one female in each group dominates reproduction, breeding principally with a single male (Clutton-Brock et al. 2001, 2006; Griffin et al. 2003; Cockburn 2004). Although many cooperative breeders are monogamous, their breeding systems differ from those of normal monogamous species in that only a small proportion of mature females breed and, in some cases, variance in breeding success is larger in females than males (Hauber & Lacey 2005; Clutton-Brock et al. 2006). In these species, overt competition for breeding opportunities can be more frequent and more intense in females than in males and traits enhancing competitive ability, such as body size, can exert a stronger effect on fitness in females than males (Reeve & Sherman 1991; Clutton-Brock et al. 2006). In several cooperative breeders, breeding females are often the largest individuals in their group and are socially dominant to all group members, playing an important role in controlling group activities and in preventing subordinate females from breeding (Reeve & Sherman 1991; Faulkes & Abbott 1997; Clutton-Brock et al. 1998, 2001; Creel & Creel 2001). In meerkats and naked mole-rats, females that acquire the breeding position also show increased levels of circulating testosterone (Faulkes & Abbott 1997; Clutton-Brock et al. 2006) as well as a period of secondary growth that is reduced or absent in males (O’Riain & Braude 2001; Russell et al. 2004; Clutton-Brock et al. 2006). Where females compete intensely for breeding status, breeders are likely to possess superior phenotypes, and the potential benefits of mate choice to males are likely to be reduced, which may explain why breeding females rarely compete to attract males and bright coloration or elaborate ornaments are normally absent.

Polygynous and Promiscuous Species

As expected, secondary sexual characters in females are usually absent or little developed in polygynous species that breed in harems. For example, in vertebrate groups where polygyny is highly developed (as in many gamebirds and ungulates), females are commonly smaller and have less-developed weaponry than males (Clutton-Brock et al. 1977, 1980; Harvey et al. 1978; Alexander et al. 1979; Plavcan 2004). In some cases where females possess obvious weapons these may be used primarily in defence against predators or in competition for resources rather than in reproductive competition: for example, antelope and deer species where females carry horns commonly live in open country where they are easily accessible to predators or in competition for resources rather than in reproductive competition: for example, antelope and deer species where competition for resources between, as well as within, sexes is common (Clutton-Brock 1982; Packer 1983). In other cases, female weaponry is used in intrasexual competition. For example, in Soay sheep, Ovis aries, where some females are horned and some are not, females with horns are more likely to initiate and win
aggressive interactions with other individuals during the lambing period than females without (Robinson & Kruuk 2007), while in some antelopes, receptive females use their horns when competing for access to males (Bro-Jørgensen 2007).

Although OSRs are usually male biased in polygynous species and reproductive competition is often more frequent or intense among males, intrasexual competition between females can also be intense, especially where they defend resources (Racey & Skinner 1979; Hawkins et al. 2002) or their social rank affects their breeding success (Silk et al. 1981; Fedigan 1983; Gilchrist 2001). In some polygynous species where female rank and breeding success are closely correlated, testosterone levels are higher in dominant than subordinate females during particular stages of the breeding cycle: for example, in spotted hyaenas, Crocuta crocuta, the rank of females is closely related to the survival of their offspring (Racey & Skinner 1979; Frank 1997; Holekamp & Smale 2000; East & Hofer 2001; Drea 2007). Heightened androgen levels may increase the ability of females to compete or to defend their young and may have evolved in these species for this reason. In breeds of domestic cattle where females have been selected for their fighting ability, they show higher levels of circulating testosterone and are usually dominant to females of breeds where females have not been selected to compete (Plusquellec & Boussou 2001). In addition, heightened androgen levels in females may affect the development of offspring (Staub & de Beer 1997). For example, in spotted hyaenas, cubs born to dominant mothers with their fighting ability, they show higher levels of circulating testosterone and are usually dominant to females of breeds where females have not been selected to compete (Plusquellec & Boussou 2001). In addition, heightened androgen levels in females may affect the development of offspring (Staub & de Beer 1997). For example, in spotted hyaenas, cubs born to dominant mothers with high concentrations of androgens in late pregnancy show higher rates of aggression as juveniles than those born to females with lower androgen levels (Dloniak et al. 2006).

In some species where dominant females show elevated testosterone levels during gestation, their genitalia show signs of masculinization (Licht et al. 1992, 1998; Drea et al. 1998; Glickman et al. 1998): spotted hyaenas are the best-known example, but genitalia of adult females show evidence of masculinization in a number of other species where females compete intensely, including several lemurs (Ostner et al. 2003; Drea 2007; Drea & Weil, in press). Masculinization of female genitalia may be a nonadaptive by-product of elevated testosterone levels or of increased sensitivity to androgens (Racey & Skinner 1979; Frank 1997). Alternatively, it may allow females to deflect aggression directed at them by dominant females or to reduce sexual harassment by males (Hawkins et al. 2002; Hofer & East 2003). For example, the striking pseudopenis and pseudoscelotrum of female spotted hyaenas closely mimic male genitalia and may allow subordinate females to mimic males, and to reduce the amount of aggression they receive from dominant females (see above, Reproductive competition between females). In some mammals where adult females are frequently aggressive to younger subordinates, younger females show transient masculinization which diminishes or disappears in adults: for example, in fossas Cryptoprocta ferox, juvenile females develop an enlarged spinescent clitoris supported by an os clitoridis and a pigmented secretion on the fur underparts which, in adults, is confined to adult males (Hawkins et al. 2002). This disappears in mature females and may help to reduce aggression from territorial females (Hawkins et al. 2002). This explanation is strengthened by evidence that, in some colobine monkeys where adolescent males are the target of intense aggression from resident males, the genitalia of male adolescents appear to show transient feminization (Kuhn 1972). In other cases, female mimicry of males serves to reduce harassment by courting males. For example, in some damselflies and a number of butterflies, females occur in two colour phases, one of which closely resembles males and andromorphic females are not harassed as frequently by courting males as normal females (Robertson 1985; Van Gossen et al. 1999, 2001).

In a number of polygynous or promiscuous animals, females possess striking ornaments that may have evolved as a result of male mating preferences. Well-studied examples include the abdominal sacs and enlarged pinnate leg scales of females in some empidid dance flies (Cumming 1994; LeBas et al. 2003) and the perineal swellings of females in social primates and some birds (Chiba & Nakamura 2002, 2003; Zinner et al. 2004; Ekstrom et al. 2007). In most (if not all) polygynous species where females are ornamented, they have access to multiple males and can gain direct benefits from courtship or mating with multiple partners. For example, in empidid dance flies where females are ornamented, males provide females with nuptial gifts, the size of a female’s ornaments reflects her fecundity and males favour highly ornamented partners (Cumming 1994; LeBas et al. 2003). Similarly, most primates where females show pronounced sexual swellings live in multimale groups where females have access to multiple partners (Clutton-Brock & Harvey 1976; Zinner et al. 2004). In many of these species, females gain support and protection for themselves and their offspring from males they consort with (de Waal 1982; Smuts 1985; Weingrill 2000; Palombit et al. 2001), and females compete for the attention of males. The size and colouring of female sexual swellings varies throughout the menstrual cycle of females, providing an approximate indicator of changes in fecundity (Plavcan 2004; Zinner et al. 2004). In addition, studies of baboons, Papio cynocephalus anubis, suggest that individual differences in the size of swellings may be correlated with individual variation in the fecundity of females and their capacity to rear offspring (Domb & Pagel 2001). It seems likely that the fat-padded breasts, thighs and buttocks of human females may have evolved for similar reasons (Mealey 2000), for, in humans, as in other primates, female secondary sexual characters are commonly used in displays that serve to attract males (Miller et al. 2007).

CONTRASTS IN THE OPERATION OF SEXUAL SELECTION IN MALES AND FEMALES

While intrasexual competition for breeding opportunities and 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 contrasts between 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 (LeBas 2006; Clutton-Brock 2007). 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 variation in resource distribution and less by variation in the form of mating systems than in males. The differences in fecundity between females generated by intrasexual competition for resources may commonly lead to large individual differences in fecundity (Clutton-Brock et al. 1982, 1988; Owens & Thompson 1994) which are likely to strengthen selection on males to identify and prefer superior partners and, on females, for signals reflecting temporal and individual differences in fecundity (Berger 1989; Reinbold et al. 2002; Clutton-Brock 2007).

There may also be qualitative differences in the costs of reproductive competition and secondary sexual characters for the two sexes. While intense reproductive competition and the evolution of increased body size in males is often associated with higher juvenile mortality and reduced longevity in males compared to females (Clutton-Brock et al. 1985), there is, as yet, no evidence that sex differences in survival are reversed in species where reproductive competition is more intense or
secondary sexual characters are more highly developed in females (Clutton-Brock 2007). One possibility is that the costs of expenditure by females on reproductive competition or ornamentation depress fecundity or parental investment, constraining the development of secondary sexual characters below the level at which they have measurable costs to female survival (LeBas 2006). For example, elevated levels of testosterone may have adverse effects on the fecundity of females or on the development of their offspring which constrain the evolution of further increases in female competitiveness (Drea et al. 2002; Knickmeyer & Baron-Cohen 2006). A few studies provide indicators that costs of this kind may occur: for example, in some populations, dominant female baboons are more likely to miscarry than subordinates and some high-ranking females have low fertility (Packer et al. 1995).

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 or natural selection. In The Descent of Man Darwin sometimes described ‘sexual’ selection as selection operating through intrasexual competition to reproduce (see above) and sometimes as selection operating through competition for mates, although the term is now most commonly restricted to selection operating through intrasexual competition for mating opportunities (Andersson 1994). Since females more commonly need to compete for breeding opportunities than mating opportunities, defining sexual selection in terms of competition for mates has the effect of restricting its operation to males, creating unfortunate dichotomies where functionally similar traits are attributed to sexual selection if they occur in males but to natural selection if they occur in females. One possible solution is to recognize an additional category of sexual selection operating through intrasexual competition for resources other than mates, such as ‘social selection’ (Crook 1972; West-Eberhard 1979, 1983, 1984, 1991; Roughgarden et al. 2006), but distinguishing clearly between ‘social’ selection and ‘sexual’ selection is likely to generate more problems than it solves (Clutton-Brock 2004; Kraaijeveld et al. 2007). The most satisfactory solution might be to abandon the distinction between sexual and natural selection altogether and emphasize, instead, the contrasting ways in which selection operates in males and females (Clutton-Brock 2004). However, the distinction between sexual and natural selection is so heavily entrenched that this is unlikely to occur and the most feasible alternative is probably to broaden the concept of sexual selection to include all selection processes operating through intrasexual competition for breeding opportunities in either sex (Clutton-Brock 2007).

CONCLUSIONS

Four main conclusions should be drawn from this review. First, secondary sexual characters are common in females as well as in males and, as in males, are commonly associated either with intrasexual competition for breeding opportunities or with competition to attract mates. Second, the relative intensity of mating competition and mate choice in the two sexes can often vary and sex differences in behaviour are probably more flexible than is commonly recognized. Third, while the distribution of secondary sexual characters in both sexes is related to the form of mating systems, the intensity of intrasexual competition in females (and the distribution of traits associated with it) may be more strongly influenced by the distribution of resources necessary to breed and rear offspring than it is in males, so that associations between the development of secondary sexual characters in females and the form of mating systems may be weaker than 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.

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Defining sexual selection as sex-dependent selection

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After almost 150 years of research, the very definition of sexual selection remains unclear. The term sexual selection was coined in 1859 by Darwin (1859), who described it in more detail in his later book (Darwin 1871), as an explanation for the evolution of those characters of males of some species that did not seem to contribute to survival in the struggle for existence, those features previously referred to by Hunter (1837) as ‘secondary sexual characters’. From that date, sexual selection has become a sexy topic that has attracted huge interest among behavioural ecologists and evolutionary biologists. However, as Clutton-Brock (2004, page 26) stated, ‘one of the problems in writing about sexual selection today is that the term is used in so many different ways’, and recent debate on the basic structure of sexual selection theory (Roughgarden et al. 2006; Kavanagh 2007; Clutton-Brock 2007) indicates that its definition has probably never been clear enough.

Darwin himself was ambiguous in the definition of the term, and was imprecise about what type of elements in the behaviour and life history of individuals should or should not be included in the sexual selection process, and how to differentiate between natural and sexual selection. Darwin initially defined sexual selection on the basis of intrasexual advantages in relation to reproduction. However, in describing the process he always referred to the advantages in relation to access to mating opportunities, either by competition with members of the same sex (in most cases males) or from the preferences of members of the other sex (mostly females; Darwin 1871). From the discussions shortly after the publication of Darwin’s book (e.g. Wallace 1889) to more recent reviews (e.g. Andersson 1994), sexual selection has generally been interpreted solely in terms of competition for mates. Only in some cases have authors extended sexual selection to other reproductive events (Møller 1994; Reynolds & Harvey 1994) or referred to the ‘narrow sense’ when using sexual selection only for competition for mates (Partridge & Endler 1987, page 272). Recently, Clutton-Brock (2007) has reviewed sexual selection, focusing especially on the operation of sexual selection in females in the context of the current debate (Roughgarden et al. 2006; Kavanagh 2007), and has proposed a return to Darwin’s initial words on sexual selection as the intrasexual competition to breed, rather than the most commonly acknowledged competition for mates.

When Darwin discussed whether certain reproductive structures were the products of natural or sexual selection, he explained that those directly connected to reproduction such as the mammary glands of mammals and abdominal pouches of marsupials in the case of females, or the receptacles for the ova in certain male fishes, were selected by natural selection. However, he also stated ‘in many cases it is scarcely possible to distinguish the effects of natural and sexual selection’ (Darwin 1871, page 257). Darwin adopted the term ‘secondary sexual characters’ (Hunter 1837) for those traits not ‘directly’ linked to reproduction, and used the qualifiers primary and secondary to assign to a given character the natural or sexual selection processes, respectively. However, the distinction between primary and secondary sexual traits was also unclear, and Darwin himself came finally to state that: ‘Unless indeed we confine the term ‘primary’ to the reproductive glands, it is scarcely possible to decide which ought to be called primary and which secondary’ (Darwin 1871, pp. 253–254). We already know that even the reproductive glands (Hosken & Stockley 2004) and the gametes (Roldan et al. 1992), at least those of males, are themselves greatly influenced by mate competition, which, since Darwin, has been the central component of sexual
selection. Therefore, distinguishing a type of selection aimed at explaining secondary sexual traits is, from its conception, imprecise, and so is the distinction between secondary and primary sexual traits.

Returning to Darwin’s wording to define sexual selection as the competition for reproduction is not theoretically consistent nowadays. This is not of course to cast doubts on the exceptional importance of Darwin’s legacy but simply to realize that we should not remain bound by the limitations existing at that time and that our understanding has moved on considerably since Darwin’s day. To Darwin, one main difference between natural and sexual selection was that natural selection affected survival in the struggle for life, whereas sexual selection arose from the competition with members of the same sex with effects not in survival but in number of offspring (Darwin 1859, 1871). However, we already know that survival, like any other elements of an individual’s life history, is simply part of a general strategy designed to pass copies of one’s own genes to the next generation. Indeed, we should focus on comparing the selection pressures operating on males and females and their consequences instead of trying to distinguish between natural and sexual selection (Grafen 1987; Clutton-Brock 2004), but an agreement on terminology is still necessary (Arnold 1994; Grant 1995).

In 1994, in an edited textbook on ethology in Spanish for University students (Carranza 1994; see also Veiga 1995), I proposed a definition for sexual selection as (page 380; translated from Spanish): ‘those natural selection forces that operate differently in males and females because of the strategies of the sexes’. This is simply to adopt the concept of sex-dependent selection as a modern use of the term sexual selection to investigate the evolution of differences between the sexes.

Competition for mates is obviously of central importance in sexual selection. Sexual reproduction provided the potential for increasing gene copies by multiple mating (Bateman 1948), so it seems clear that mating competition was at the origin of the evolutionary divergence leading to the existence of the two sexes (Bulmer & Parker 2002). However, responses to selection acting in each sex produce new selective scenarios, so that the consequences give rise to new components of selection. Female preferences, for example, might, to a great extent, be regarded as a consequence of sexual selection, as far as such preferences may have been promoted by the pre-existing competition between males for mates, although they are, indeed, elements of sexual selection in their own right. Similarly, divergent selection fuelled by mating competition has led to differences between the sexes in many other elements of their life histories, such as feeding behaviour and habitat use (Clutton-Brock et al. 2001), immune function (Marriott & Huet-Hudson 2006); growth and mortality (Clutton-Brock 1991) or senescence (Carranza et al. 2004; Carranza & Pérez-Barbería 2007; Bonduriansky et al. 2008). Such differences between the sexes are not only the consequences of selection but also causes of sex-dependent selection since they affect the sex-differential fitness effects of many phenotypic traits.

A relevant theoretical basis in support of the view proposed here is that, under sexual selection, genes successively experience different selective scenarios when carried by males and females during the evolution of a lineage. Darwin (1871) and Wallace (1889) themselves were already concerned with the heritability and expression of characters in males and females. In many cases in polygynous species it seems that males and females belong to ‘different species’. What is remarkable is that this different selection takes place despite males and females sharing (except for a small part of the sex chromosomes) the same gene pool. Genes subjected to sexual selection may either tend to increase or decrease in frequency after being in male or female bodies (Foerster et al. 2007), unless their expression becomes adequately regulated to be dependent on the male or female environments, as current genome research increasingly shows to be the case for many genes affecting the whole organism (e.g. Drosophila: Ranz et al. 2003; mice: Yang et al. 2006). Not only ornaments and weapons, but also organs not previously considered as ‘sexual’, such as liver, adipose, muscle or brains, experience the effects of sex-differential gene expression (Yang et al. 2006). We may say that natural selection becomes sexual selection when the fitness effects of genes change from a previous evolutionary stage as a consequence of the strategies of one or other sex within a species, thus leading to a situation in which the genes have to face different selective scenarios depending on sex.

We might say that, under this definition, almost all selection is sexual selection. In fact, once sexual reproduction appeared and the existence of two sexes became the typical situation for many species, sexual selection may have become a widespread type of selection affecting most traits. This is, however, the common situation only for large and familiar animals, especially vertebrates, and to some extent flowering plants, but not for many other organisms such as ciliates, seaweeds, foraminifers or yeasts. Natural selection is universal for living things. However, sex has become widespread in nature and so has its influences on selection.

Sexual selection as selection related to sex can be identified in all cases when there are two sexes or two sexual functions. The two sexual functions (and sexual selection) may occur within the same organism in hermaphrodites (Leonard 2006), either animals or plants (Arnold 1994). In other cases, sexually selected strategies may converge into similar patterns in monogamous species. This may indeed hamper the identification of sexual selection but, as for any evolutionary convergence, the key is the evolutionary history of the strategy in each sex. If sex strategies were always identical, selection would probably never be related to sex. Sex-dependent selection may also be a good way of unifying the concept of sexual selection for animals and plants (Arnold 1994). Sexual selection cannot be identified as mere differences in selection intensity between males and females, but rather in the nature of the trait–fitness relationships in each sex. Sexual selection acting on each sex or sexual functions leads to the differentiation of phenotypes, producing sex-specific traits or sexual versions of many traits. These sex traits were historically classified as primary or secondary, although I believe that this distinction should not be maintained.

Although there is only one selection process, we can, indeed, maintain a practical differentiation between natural and sexual selection. In the evolution of any trait we may identify forces of natural selection and then look at how they have been modulated because of the strategies of the sexes. We may refer to specific selection modes such as signal selection, fecundity selection, mating selection, including intrasexual competition for mates and mate choice, as well as postcopulatory competition including sperm competition and cryptic mate choice, when describing how selection acts in each sex, but use sexual selection as the general term that refers to selection acting differently in each sex or sexual function, favouring adaptations that facilitate the sex-specific differentiation of phenotypes. In conclusion, I suggest that extending sexual selection to sex-dependent selection may help to unify modern research on Darwin’s original idea of ‘selection in relation to sex’.

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Sexual selection is one of Darwin's major contributions to evolutionary biology. However, it has been subjected to repeated controversy, including our own recent challenge (Roughgarden et al. 2006), which has provoked lively debate (Kavanagh 2006; Clutton-Brock 2007). In response, Clutton-Brock (2009) proposes to extend the theory of sexual selection to females in a manner parallel to that for males, and Carranza (2009) proposes to redefine sexual selection theory. We refer to both of these proposals collectively as ‘Sexual Selection 2.0’.

In this paper we show that Clutton-Brock’s extension of the theory to females exacerbates the problems with standard sexual-selection theory, compounding the errors already present when the theory is applied specifically to males. We also show that Carranza’s redefinition of sexual selection violates the basic canon of science that once a hypothesis has been falsified, it shall not be redefined to render it true in light of new data, a process that, if allowed, would render any hypothesis infinitely malleable and thus untestable. Overall, we find that replacing the standard theory of sexual selection with some updated version 2.0 is inadvisable. Instead, we note that our proposal for an altogether new theory to replace sexual selection avoids compounding existing errors, is testable, and is possibly correct.

Below, we consider the two papers separately.

EXTENDING SEXUAL SELECTION TO FEMALES

The crux of the difficulty with Clutton-Brock’s proposal is stated in the abstract in which he writes, ‘Since 1871, a substantial body of research has confirmed his [Darwin’s] explanation of the evolution of secondary sexual characters in males’. This claim, although widely believed, is not true. Research has not confirmed Darwin’s theory of sexual selection in males.

Chapter 2 of The Genial Gene (Roughgarden 2009) details three categories of objections to sexual selection theory. The first category consists of the many exceptions to the promiscuous-male and choosy-female templates that Darwin stipulates as ‘nearly universal’ subject only to ‘rare exception,’ as summarized in 2004 in Evolution’s Rainbow (Roughgarden 2004). Sexual selection advocates dismiss...
these exceptions because sexual selection is supposedly true in a great majority of cases. None the less, the variety and quantity of exceptions are now known to be enormous and invite suspicion that sexual selection theory was on the wrong track to begin with.

The second category consists of studies that have appeared since 2004 based on species that were not thought to be exceptional to the promiscuous-male and choosy-female templates, species that possessed what were thought to be typical showy secondary sexual characters in males. In *The Genial Gene*, these species are termed ‘poster-child species.’ For these species extensive data have, according to the studies’ authors, refuted sexual selection predictions or expectations. Failed poster-child species include the collared flycatcher, *Ficedula albicollis* (Qvarnström et al. 2006), the blue tit, *Cyanistes caeruleus* (Hadfield et al. 2006), the barn swallow, *Hirundo rustica* (Bro-Jørgensen et al. 2007), the lark bunting, *Calamospiza melanocrorys* (Chaine & Lyon 2008), the peacock, *Pavo cristatus* (Takahashi et al. 2008), swallowtail butterflies (Papilionidae; Kunte 2008) and dragon lizards (Agamidae; Ord & Stuart-Fox 2006; see also a meta-analysis of extrapair parentage, Akçay & Roughgarden, 2007b). Furthermore, the classic studies of Bateman (1948), cited by both Clutton-Brock and Carranza, have been thoroughly discredited by three independent critiques (Tang-Martinez & Ryder 2005; Dewsbury 2005; Snyder & Gowaty 2007). It is not an exaggeration at this time to say that every species studied with sufficient care and rigour fails to confirm sexual selection theory and that, despite the thousands of papers over the years that invoke the sexual selection narrative to explain their results, evidence for sexual selection remains inconclusive and sexual selection remains undemonstrated in any single case.

The third category consists of logical, often population-genetic, contradictions to the sexual selection story. Notable among these is the ‘paradox of the lek’, which can be circumvented only by postulating far-fetched and untested schemes for replenishing the bad genes in males that female choice is presumably weeding out each generation. Without a continual supply of bad genes in males, continual female choice for male genetic quality is pointless. As of 2007, 10 distinct hypotheses to circumvent the paradox of the lek had been proposed (Miller & Moore 2007). In 2008, two more attempts at circumvention appeared as well (Harris et al. 2008; Kotiaho et al. 2008). The growing literature of the past dozen years aimed at ‘resolving’ the paradox of the lek is itself testimony that the paradox has not been resolved. It cannot be resolved. The paradox of the lek is a fatal flaw of sexual selection theory. Another population-genetic contradiction detailed in *The Genial Gene* is that the fitness difference between a ‘good’ and ‘bad’ male is extremely small and undetectable according to the population-genetic theory of how weakly deleterious mutations accumulate.


Thus, Clutton-Brock’s confident assertion that sexual selection is well established for males and therefore ripe for extension to females is unwarranted. None the less, Clutton-Brock’s review surveys reproductive behaviour in females and proposes to extend the definition of sexual selection to encompass ‘all selection processes operating through intrasexual competition for breeding opportunities in either sex’ (Clutton-Brock 2008, page 6). Clutton-Brock argues that even in non-sex-role-reversed species, sexual selection in females mirrors that in males, operating through male mate choice and intrasexual contests. The only major distinction is that females might compete more for resources than males do, as well as for mates, thus implicitly endorsing the dubious assumption that females invariably have the higher parental investment.

Clutton-Brock’s version of Sexual Selection 2.0 amounts to saying that there is intra- and intersexual competition simultaneously in both sexes. If we add sexual conflict to this mix and assume that it too operates in both directions, then we are left with the simple position that every animal is always competing with every other animal. Such a theory is devoid of any specific meaning.

Moreover, awarding females parity in the eye of sexual selection transfers to females the problems of the male-based sexual selection theory. The paradox of the lek for females (termed ‘the paradox of the crèche’ in *The Genial Gene*) is the dilemma of replenishing the bad genes in females that male choice is presumably weeding out each generation. Although data in some species might show a bit of male choice of females simultaneous with female choice of males, the rationale that such choice is to acquire genetic benefits has not been shown and is almost surely false. Instead, choice for direct benefits by either sex amounts to the negotiation that underlies cooperation and bargaining, the very negotiation that our own theory focuses on.

Finally, the Clutton-Brock position unwittingly abandons any connection between gamete size and sex role, a connection that sexual selection advocates have taken as fundamental. If both males and females are equally choosy, as Clutton-Brock proposes, then gamete size is irrelevant to sexual selection, leading to yet another logical inconsistency in the standard theory. In sum therefore, we find Clutton-Brock’s proposal for a Sexual Selection 2.0 to be untenable.

**REDEFINING SEXUAL SELECTION**

In contrast to Clutton-Brock, Carranza acknowledges difficulties with present-day sexual selection theory. Indeed, his first sentence states, ‘After almost 150 years of research, the very definition of sexual selection remains unclear’. The definition of descent through modification from common ancestors and the definition of natural selection, which together are the bedrock of evolutionary theory, are not unclear; only sexual selection theory suffers conceptual malaise. Carranza notes that Darwin originally defined sexual selection quite generally as selection in relation to reproduction, to be contrasted with selection in relation to survival.

Despite this initial generality, Carranza further notes that ‘in describing the process he [Darwin] always referred to the advantages in relation to access to mating opportunities, either by competition with members of the same sex (in most cases males) or from the preferences of members of the other sex (mostly females)’. In practice, Darwin’s picture of sexual selection was specifically about mating advantages and, as such, offers an explanation for secondary sexual characters that could be true or false empirically. That is, the secondary characters might relate to mating success, as he hypothesized, or could relate to other considerations such as offspring-rearing success, as we hypothesize.

The beauty of Darwin’s formulation is that it is a genuine scientific hypothesis subject to falsification. If it is false, then be it, if true, then so be that too. Redefining sexual selection so that it becomes no longer falsifiable disqualifies sexual selection as a scientific hypothesis and, if permitted, would undercut the scientific credibility of behavioural ecology. But Carranza takes this tack.

Carranza writes, ‘Darwin’s wording to define sexual selection as the competition for reproduction is not theoretically consistent nowadays’. So Carranza defines ‘sexual selection as “those natural selection forces that operate differently in males and females because of the strategies of the sexes”’. He writes that natural selection becomes sexual selection when ‘genes have to face
different selective scenarios depending on sex' and goes on to state that 'under this definition, almost all selection is sexual selection'. Carranza does sexual selection no favour. In an effort to render it always true by definition, he destroys sexual selection's standing as a scientific hypothesis. Thus, we do not find Carranza's proposal for a Sexual Selection 2.0 to be tenable either. Instead, we retain the original statement of Darwin's theory of sexual selection and find the data available today sufficient to regard it as having been falsified.

**COMPETITION, COOPERATION AND SOCIAL SELECTION**

Our position is that the greatest scientific progress will now be made by offering alternative hypotheses in place of sexual selection. We conceive of a reproductive social group as the biological equivalent of a firm in economics, a firm whose product is offspring. Thus, our focus is not on mating success, but on offspring-producing success. Members of a reproductive social group must work as a team, and we see reproductive social behaviour, including mate choice and reproductively relevant traits such as secondary sexual characters, as revolving around what must be done by individuals to join a team, to coordinate actions in the team and to discern and pursue a team goal.

Central to our proposed theory to replace sexual selection is a conceptualization of social evolution with two ‘tiers’, one behavioural and the other population genetic. In contrast, the theory behind sexual selection conceives of social evolution in a single tier, as exemplified by the evolutionary game theory started by Maynard Smith (1982). This requires that behavioural dynamics coincide with gene-pool dynamics, which precludes using modelling tools such as cooperative game theory to describe behaviour because the gene-pool dynamics are purely competitive, culminating in an evolutionarily stable strategy (ESS). Instead, splitting the overall process into two tiers allows the lower (behavioural) tier to be governed by cooperative outcomes such as the Nash bargaining solution (Nash 1950), as well as by the familiar Nash competitive equilibrium, whereas the upper (population-genetic) tier remains governed by purely competitive dynamics leading to the ESS. We have termed this approach ‘social selection’, which is different from other uses of the phrase by Crook (1972) and West-Eberhard (1979).

Because our original proposal for a new theory to replace sexual selection (Roughgarden et al. 2006) drew much criticism at the time, and still does, two anonymous referees have requested that we address the criticisms to our theory. In the absence of answers to our critics, the referees suggest that attempts to revise sexual selection into version 2.0 would be preferable to its wholesale replacement, or even that the standard version should be consigned OK as it currently stands. Of our proposal for a new theory, one referee notes ‘how widely the scientific community disagreed with it’ and another referee wonders what could produce a ‘shift in the consensus view of sexual selection towards the views of the authors [us]’. Well, we responded to the criticisms when they appeared (Kavanagh 2006; see also our online responses on the Science Web site and other venues). For the most part, the criticisms have been emotional and less than useful in contributing to constructive discourse. Today, our most recent overall position, including our response to critics, is summarized in *The Genial Gene* (Roughgarden 2009; cf. book reviews in Belden 2009, Odling-Smee 2009, Pruett-Jones, in press and video-blog interview with Robert Wright on 19 April 2009 at http://bloggingheads.tv/diavlogs/0526). We note also that consensus is a ‘lagging indicator’, describing what people have thought in the past, whereas criticism is a ‘leading indicator’, describing what people might think in the future. The truth of sexual selection will not be decided by vote or consensus, but by the facts. And it is the facts that are sinking sexual selection. The enormous and still growing evidence against sexual selection is what motivates our call for a new theory and our efforts to provide one. Yet, sexual selection advocates routinely ignore or misinterpret our findings. As an example, our meta-analysis that casts serious doubt upon the validity of good-genes or compatible-genes benefits in avian extrapair paternity (Akçay & Roughgarden 2007b) is either ignored entirely (Griffith & Immler 2009) or worse, cited as supporting these hypotheses (Gangestad & Thornhill 2008). Thus, our position may be far more consistent with available data than the ‘consensus’ appreciates.

Instead of engaging in continuing polemic, our lab has been developing a new theory for sexual reproduction that we term social selection. Concerning the genetic system, Iyer & Roughgarden (2008b) have shown that the basic difference between male and female gamete sizes (anisogamy) can evolve to maximize the contact rate between gametes and represents a mutually beneficial state with regard to the male and female functions. This result counters the established theory attributed to Parker et al. (1972) that anisogamy results from males reducing investments in gametes and thus parasitizing female investment, which is the source of claims that sexual conflict must underlie all sexual reproduction (Parker 2006). Similarly, Iyer & Roughgarden (2008a) show that the evolution of male and female bodies (dicyc) may reflect a specialization to increase fertilization rates. These papers show that nonconflicting selection on the sexes can potentially explain the most basic features of the genetic system for sex. Another study investigates the origin of alternation of generations in plants as a mechanism to increase fertilization rates (Iyer & Roughgarden 2009).

Concerning behaviour, as already mentioned, we introduced a two-tier approach to modelling social behaviour (Roughgarden et al. 2006) in place of the single-tier ESS framework from Maynard Smith (1982). The two-tier framework allows cooperative game theory, including Nash bargaining, to be used in the behavioural tier. Our work also explores how cooperative dynamics can explain why bird species often have extrapair paternity. The canonical explanation for extrapair paternity, namely that females have extrapair copulations with genetically superior males, has failed in empirical tests (Arnqvist & Kirkpatrick 2005; Akçay & Roughgarden 2007b). We propose instead that extrapair parentage might represent reproductive transactions between males in exchange for pairing with females that have higher breeding success (Akçay & Roughgarden 2007a). Similarly, in species with biparental care, experiments that manipulate parental effort fail to confirm the predictions of cooperative parental care theory (Hinde 2006). We have shown that this discrepancy can be explained by modelling the parents as working together as a team to maximize nest production (Akçay & Roughgarden 2009). In a model that combines both the behavioural and the evolutionary tiers, we have shown that even with strict payoff–conflict between individuals, individual-level natural selection can lead to other-regarding motivations (Akçay et al. 2009). Manuscripts soon to be submitted include studies of the evolution of ornaments, sexual dimorphism and sexual polymorphism (P. Iyer & J. Roughgarden, unpublished data); the evolution of the payoff matrices for behavioural-tier dynamics (E. Akçay & J. Roughgarden, unpublished data); and the evolution of parent–offspring relations using management science theory for the optimal incentive policy in a conglomerate (J. Roughgarden & Z. Song, unpublished data).

**CONCLUSION**

In conclusion, we appreciate the contributions by Clutton-Brock and Carranza to the debate on the future of sexual selection theory. Few people apprehend how grave the deep, broad difficulties are for...
sexual selection, and we interpret the Clutton-Brock and Carranza proposals as implicitly acknowledging this situation. However, we also think that neither Clutton-Brock nor Carranza resolves the problems sexual selection theory is facing because the problems are simply unsolvable. Rather than issue a new version of sexual selection, Sexual Selection 2.0, alternatives to the entire theoretical approach may be preferable. We invite readers to consider the alternative approach we have proposed, social selection.

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Forum

We do not need a Sexual Selection 2.0—nor a theory of Genial Selection

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SEXUAL SELECTION IN MALES

We have no need of a Sexual Selection 2.0 and, despite Roughgarden and Akçay's assertions (Roughgarden & Akçay 2010), I have never suggested that we did. Roughgarden and Akçay believe that the theory of sexual selection is fundamentally flawed and should be abandoned. Their attack on sexual selection rests on three main planks, all of them shaky. First, they point to irregularities, inconsistencies and anomalies in relationships between the characteristics of females and males and sex differences in investment in gametes and offspring (Trivers 1972), in potential rates of reproduction (Clutton-Brock & Parker 1992), and in variance in breeding success (Wade & Arnold 1980; Clutton-Brock 1988; Clutton-Brock et al. 1988). While these certainly exist, they have been recognized for many years (Campbell 1972; Clutton-Brock 1983; Andersson 1994; Gowaty 2004; Kappeler & van Schaik 2004) and are an integral part of the modern theory of sexual selection, showing us how sexual selection operates in different systems. They are refinements not flaws and do not undermine sexual selection theory.

Second, Roughgarden and Akçay attack evidence of sex differences in reproductive variance, exaggerating criticisms of Bateman's original study of sexual selection in Drosophila. Bateman (1948) argued that mating with multiple partners had no effect on the reproductive success of females but a strong effect on reproductive success in males whereas subsequent work has shown that mating with two or three partners increases the reproductive success of females (Tang-Martinez & Ryder 2005; Snyder & Gowaty 2007). However, Bateman's fundamental principle remains intact. In many species, the number of mating partners typically has a stronger effect on fitness in males than females and variance in breeding success is higher and selection for traits that improve access to breeding partners is stronger in males (Clutton-Brock 1988; Jones et al. 2000, 2002; Lorch 2002, 2005; Becher & Magurran 2004; Rios-Cardenas 2005; Mills et al. 2007; Webster et al. 2007; Lorch et al. 2008).

The third plank of their case against sexual selection rests on criticisms of sexual selection operating through female mating preferences. Here, they argue that female mating preferences are bound to remove genetic variance in male fitness although there is extensive evidence that this need not be the case (Andersson 2004; Miller & Moore 2007), ignoring many of the most comprehensive studies of pre- and postcopulatory female choice (Andersson 1982; Hoglund et al. 1990; van Rhijn 1991; Wilkinson & Dodson 1997).

They review five empirical studies of birds where they suggest that evidence fails to support the predictions of sexual selection theory. Of the five species, three are biparental, monogamous species where the magnitude of sex differences in breeding competition and mate choice is likely to be relatively small. In one of the remaining two (lark buntings) they suggest that evidence that sexual selection on male phenotypic traits varies between years is incompatible with the theory of sexual selection, which is not the case. In the other (peacocks) they cite the results of a recent study that failed to find evidence of consistent female preferences for train (tail) size in males but fail to mention the results of other studies of the same species that have provided evidence of female preferences for males' elaborate plumage (Petrie et al. 1991; Yasmin & Yahya 1996; Loyau et al. 2005a, b, 2007, 2008).

Even if we accept Roughgarden and Akçay's critical assessment of the evidence of sexual selection operating through precopulatory female choice (which I don't), there remains the first mode of sexual selection, Darwin's 'law of battle'. What about the classical examples of the operation of sexual selection through intrasexual competition? Do Roughgarden and Akçay believe that males do not regularly compete in horned beetles and water spiders, bullfrogs,
pheasants, lions, seals and elephants and that intrasexual competition has played no part in the evolution of male characteristics in these species (Le Boeuf 1974; Borgia 1979; Eberhard 1979; Alexander et al. 1979; Clutton-Brock et al. 1979, 1988; Harcourt et al. 1981; Davison 1985; Conner 1988; Le Boeuf & Reiter 1988; Kruuk et al. 2000, 2002)? There is enormous evidence to the contrary (Andersson 2004). And how do they account for consistent relationships between the development of competitive traits in males and the degree of polygyny (Clutton-Brock et al. 1977, 1980; Harvey et al. 1978; Alexander et al. 1979; Harcourt et al. 1981)?

**SEXUAL SELECTION IN FEMALES**

In the first part of their article, Roughgarden and Akçay focus their criticisms on my unremarkable suggestion that, to understand the evolution of sex differences in behaviour and morphology, we need to understand the operation of sexual selection in females as well as in males (Clutton-Brock 2009). They argue that the recognition of sexual selection in females leaves a theory that is ‘devoid of any specific meaning’, but do not say why. If sexual selection does not operate in females, how do they explain the evolution of elaborate plumage in females in many polyandrous birds (Eckmann 1983; Davison 1985; Amundsen 2000a) or the conspicuous perineal swellings found in females in a number of primates and birds where females have access to more than one potential partner (Clutton-Brock & Harvey 1976; Zinner et al. 2004), or the breasts of human women (Caro 1987; Caro & Sellen 1990)?

Roughgarden and Akçay appear to believe that the idea that sexual selection operates in females is novel and represents a new version of the theory of sexual selection. It isn’t and doesn’t. Darwin was well aware that sexual selection operates in both sexes, although he was principally concerned with its operation in males. Here he is on the evolution of sex differences in button quail: ‘Taking as our guide the habit of most male birds, the greater size and strength as well as the extraordinary pugnacity of the females of the Turnix and emu must mean that they endeavour to drive away rival females, in order to gain possession of the male; and on this view, all the facts become clear; for the males would probably be most charmed or excited by the females which were most attractive to them by their bright colours, other ornaments or vocal powers. Sexual selection would then do its work, steadily adding to the attractions of the females; the males and young being left not at all or but little modified.’ (Darwin 1871, page 480).

Research over the last 10 years has greatly extended our knowledge of the operation of sexual selection in females (Amundsen 2000a; Domb & Pagel 2001; Houde 2001; LeBas et al. 2003; Heinsohn et al. 2005; LeBas 2006; Wright et al. 2008). There is now extensive empirical evidence that females as well as males often compete intensely for breeding opportunities (Eckmann 1983; Simmons 1995; Holekamp et al. 1996; Kvarnemo & Simmons 1999; Berglund & Rosenqvist 2003); that males, as well as females, can show persistent preferences for breeding with particular categories of partners (McLennan 1995; Amundsen & Forsgren 2001; Pizzari et al. 2003; Wong & Jennions 2003; Herdman et al. 2004; Griggio et al. 2005); and that both these processes affect the evolution of behaviour and morphology in females (Davison 1985; Amundsen 2000a; Amundsen & Forsgren 2001; Heinsohn et al. 2005; Rubinstein & Lovette, in press).

Although we now understand more about the operation of sexual selection in females, it has still received much less attention than sexual selection in males and there are still basic conceptual issues to be sorted out. One of them concerns which evolutionary processes operating in females should be regarded as examples of sexual selection and which should be treated as examples of natural selection. The problem here is that many recent definitions of sexual selection restrict it to evolutionary processes operating through competition for mates (Andersson 2004), while intrasexual competition between females is often over breeding opportunities or resources rather than mates or mating opportunities (West-Eberhard 1979; Clutton-Brock 2007, 2009). To solve this problem, it is sometimes suggested that we need an additional category of ‘social’ selection to include cases where individuals compete with members of the same sex for resources necessary for reproduction rather than for mates (West-Eberhard 1975, 1979). However, this has the disadvantage that it can lead to similar traits that have evolved through fundamentally similar processes being attributed to sexual selection if they occur in males and to social selection if they occur in females. A further problem is that males as well as females often compete for resources that are necessary to rear offspring (including breeding sites, feeding territories and parental care). In addition, in many systems where females compete for access to males, they are probably competing for resources in the form of parental care rather than for access to gametes. Distinguishing clearly between sexual and social selection is seldom easy in either sex.

To avoid these difficulties, my own preference is to abandon any formal attempt to distinguish between natural and sexual selection and to focus on contrasts in the components, intensity and targets of selection between males and females (Clutton-Brock 1983, 2004, 2009). Another solution is to define sexual selection as operating through individual differences in breeding success generated either by intrasexual competition or by intersexual mate choice, so that it encompasses the consequences of reproductive competition and mate choice in both sexes (Clutton-Brock 1983, 2004, 2009). Views differ and I recognize that there is a discussion to be had over this but these are not grounds for dismissing the operation of sexual selection in females.

**GENIAL SELECTION**

If we have no need of a Sexual Selection 2.0, still less do we need to replace the theory of sexual selection with Roughgarden and Akçay’s vague and amorphous concept of social selection. As they are using the term to refer to a very different concept to West-Eberhard (1979, 1983) and social selection has been used in several other ways (Tanaka 1996; Moore et al. 2002), I shall follow Roughgarden’s practice of giving a convenient label to arguments that she is commenting on and shall refer to the processes she describes as Genial Selection, in line with the title of her recent book, *The Genial Gene* (Roughgarden 2009).

Genial Selection has recently been described by Michael Ruse in his review of Roughgarden’s book as a ‘warmer and friendlier way of thinking’ (Ruse 2009). It consists of an explanation of reproductive behaviour and the evolution of sex differences based on two-tier models of selection involving mutualistic interactions between individuals that maximize their reproductive output (Roughgarden et al. 2006; Roughgarden 2009). When Roughgarden originally presented Genial Selection as an alternative to sexual selection (Roughgarden et al. 2006), her claims provoked 40 evolutionary biologists to write in to take issue with her arguments (Kavanagh 2006). Their criticisms were detailed, closely reasoned and extensive and there is no space to repeat them here: anyone interested should read the original commentaries. The theoreticians argued that her theoretical arguments were not novel and what was new was wrong. The empiricists objected to criticisms of sexual selection, the selective use of examples and the distortion of arguments and evidence. Here, Roughgarden and Akçay repeat their original arguments and dismiss the responses of Roughgarden’s original critics as ‘emotional’, but make no attempt to answer them.
The principal problem with Genial Selection lies in Roughgarden’s claim that it provides an alternative to the theory of sexual selection rather than in the detailed structure of her models. Mutualistic interactions between the sexes are not uncommon, especially in monogamous, biparental species, and are capable of generating strong selection for cooperation between breeding partners and complex processes of negotiation over relative levels of investment (Davies & Hatchwell 1992; Davies et al. 1996; Kokko et al. 2001). Although recognition of these processes is not novel, they may not have attracted the attention they deserve, so the development of theory in this area may be useful. But this does not suggest that competition to monopolize or attract mates is not common, too, and sexual selection theory provides ways of establishing the extent to which intersexual interactions are mutualistic or antagonistic (Parker 1979, 2006; Pizzari & Snook 2003, 2004; Shuster & Wade 2003). While Genial Selection may add to our understanding of the behaviour of males and females in particular circumstances, unlike the theory of sexual selection, it provides no general explanation of the evolution and distribution of sex differences in behaviour, physiology and morphology.

In summary, Roughgarden and Akçay’s rejection of sexual selection is based on restricted definitions, distorted arguments and 18–20- even wrong evidence. Their belief that sexual selection is confined to males, their view that its recognition in females is novel and their extravagant claim that Genial Selection represents an alternative to sexual selection are all incorrect. Since the arguments that they summarize in this paper have already been published twice (Roughgarden et al. 2006; Roughgarden 2009) and have attracted extensive critiques that have not yet been answered (Roughgarden et al. 2006; Roughgarden 2009), it is surprising that they are being republished again here. Is it really the case that the Editorial Board of Animal Behaviour believe that Roughgarden and Akçay have now made a convincing case that ‘research has not confirmed Darwin’s theory of sexual selection’ or that ‘sexual selection remains unconfirmed in any single case’?


References


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Evolutionary theory has experienced big changes since Darwin published his book on the origin of species (Darwin 1859). New elements such as the development of genetic theory (Fisher 1930; Wright 1931; Haldane 1932; Dobzhansky 1937), recognition of selection at the level of genes (Williams 1966) and kin selection (Hamilton 1964) have been incorporated to refine and adapt the new natural selection theory. As a consequence, when we now use the term natural selection in an academic context we refer to processes resulting in changes in gene frequencies rather than ‘preservation of favoured races in the struggle for life’ or ‘survival of the fittest’.

Darwin also appreciated a distinctive form of selection, which he invoked to explain sexual dimorphism, referring to it as ‘selection in relation to sex’ (Darwin 1871). He was, however, ambiguous when describing the process, initially considering that it derived from competition for reproduction, but later recognizing the process as mediated through competition for mates, which has become the most widely accepted definition for sexual selection (e.g. Andersson 1994). By contrast to our understanding (and revision) of the theory of natural selection, it seems that sexual selection has been little updated. Considerable empirical and theoretical effort has focused on studying trait evolution through mate choice (e.g. Mays & Hill 2004; Andersson & Simmons 2006), or explaining the recurrent problem of the lek paradox (e.g. Kotiaho et al. 2008). Notable advances such as sexual selection in plants (Shuster 2009) and postcopulatory sexual selection (Eberhard 2009) have helped fill early gaps. However, it is remarkable that the basic concept of sexual selection has scarcely been revised after the revolution in our understanding of natural selection.

In a recent opinion article (Carranza 2009) I proposed we should return to Darwin’s initial idea of ‘selection in relation to sex’ but, because our understanding has moved on considerably since Darwin’s day, we should not feel trapped by the details of his original suggestions of the processes involved. I suggested that what is remarkable in the light of current knowledge is that under sexual selection, genes successively experience different selective scenarios when carried by males and females during the evolution of a lineage, and that these different scenarios are what actually shape sexual dimorphism. Thus, I proposed ‘sex-dependent selection’ as a modern use of the term sexual selection to focus on the selection pressures operating differently on males and females and their consequences. I do not see this interpretation different enough to Darwin’s description to deserve differentiation from his theory; rather it is an updating of it, in exactly the same way as our understanding of Darwin’s theory of natural selection has been refined and revised. I agree that intrasexual competition for mates (including broad-sense mate choice and postcopulatory selection) is a very important component of sexual selection (and it is perhaps at the root of the whole process). Also, my proposal includes competition for breeding opportunities (Clutton-Brock 2007, 2009) as far as it differs in males and females. However, competition for mating or breeding commonly affects many aspects of life history.
that were traditionally regarded as not being sexual selection (Ranz et al. 2003; Marriott & Huet-Hudson 2006; Yang et al. 2006). As for natural selection, the conceptual boundary that I propose is at the level of genes, that is, using sexual selection as ‘selection in relation to sex’ or ‘sex-dependent selection’ to refer to the differences in selective scenarios that any gene of a sexual species may face in being carried by one or other sex during evolution, since this is what actually shapes the differences between male and female phenotypes within a species.

Roughgarden & Akçay (2010; hereafter R&A) criticize this position by making two points. On the one hand they defend their proposal (Roughgarden et al. 2006) of replacing sexual selection by social selection. This idea may need discussion in the scientific community (as has already begun: Kavanagh 2007). However, although I do not myself concur with this suggestion, it is not my objective in this short note to provide arguments against it. On the other hand, R&A worry about the proposals by Clutton-Brock (2009) and myself (Carranza 2009) because they do not accept any development of the original Darwinian theory of sexual selection from what was originally described. To defend their position they have gone too far by saying that my proposal of updating sexual selection ‘violates the basic canon of science that once a hypothesis has been falsified, it shall not be redefined’. Sexual selection theory (note that R&A prefer to rate it as a hypothesis when rejecting my proposal) has not been falsified but greatly supported in its essentials. R&A seem not to admit that any theory may need refinement by the addition of new elements as scientific knowledge advances. Rather, they prefer to maintain the theory as it was almost 150 years ago and try to rebut it today. With the same procedure, we could falsify the 150-years-old natural selection theory, because Darwin’s original conception that it was the survival of the fittest that caused evolutionary change offered an inaccurate and incomplete explanation of a more complex process. However, the essentials of Darwinian description of natural selection are not only still valid but also constitute the basis for all modern evolutionary biology, although it is also true that our understanding of the process has been repeatedly updated and redefined (Fisher 1930; Haldane 1932; Dobzhansky 1937; Hamilton 1964; Williams 1966; Dawkins 1982). Sexual selection, as an element of natural selection, deserves the same treatment, although R&A might surprisingly think that this ‘would undercut the scientific credibility of behavioural ecology’.

R&A also made an out-of-context citation of my phrase ‘under this definition, almost all selection is sexual selection’. They omit the previous part of the sentence ‘We might say that’. I used this rather extreme statement to introduce the reasons why I think that this is not the case for many species and that it may be accurate in cases when sexual selection has affected most life history traits. Rather than doing ‘sexual selection no favour’, as R&A state, this is simply to realize the power of sexual selection in influencing so many elements of life histories.

Finally, I would like to stress that my proposal was not designed as an alternative to R&A’s work, as they seem to suggest. R&A are free to propose a replacement if they want, but the view I propose for sexual selection is not meant to solve any potential problem of sexual selection theory that they might have raised, as I think that the problems with the theory R&A present do not exist. Nevertheless, I acknowledge that R&A have criticized my proposal on sexual selection, because I believe that discussion is not only enriching but also essential to the advancement of scientific ideas.

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References


Forum

Sexual selection: endless forms or tangled bank?

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Few people apprehend how grave the deep, broad difficulties are for sexual selection

Roughgarden & Akçay 2010

For some biologists sexual selection is in trouble. For the first time since the reinvigoration of sexual selection in the 1970s following the effective rediscovery of mate choice (Bateson 1983; Bradbury & Andersson 1987), the validity of sexual selection as a central component of modern evolutionary theory is being challenged (Roughgarden et al. 2006). That paper, in which Roughgarden and colleagues boldly stated that sexual selection was ‘wrong’, caught evolutionary biologists on the hop (Kavanagh 2006). Since then renewed versions of the challenge to sexual selection have appeared (e.g. Roughgarden 2007; Roughgarden & Akçay 2010), and, as will be obvious from the companion pieces to this article, resolution is still some way off. In addition, core aspects of the theory of sexual selection, including its definition, have also received renewed attention (Clutton-Brock 2007, 2009; Carranza 2009). Here I consider the current status of sexual selection and attempt to make five points. First, sexual selection is best considered as a useful subset of the overall process of natural selection, with which biologists seek to understand the evolution of traits associated with competition for mates. As such, sexual selection shares the logical framework and coherence of its twin sister, natural selection. Second, the collection of theory (which I will term ‘mating systems theory’) used in part to predict patterns of sexual selection is not the same as sexual selection itself; mating systems theory attempts to predict how aspects of a species’ biology (from its physiology through to ecology) determine what patterns of competition for mates occurs, and whether or not this differs between the sexes (if ‘sexes’ even exist). Mating systems theory is therefore conceptually analogous to aspects of population ecology theory that predict how organisms compete for other resources, thereby driving natural selection. Third, the action of sexual selection does not depend on whether or not behavioural interactions between mating partners during reproductive episodes are considered cooperative or selfish. Fourth, whether or not there is sexual selection does not depend on what ‘roles’ different reproductive classes (mating types or sexes) take during reproductive interactions. Fifth, the claim that there is no evidence for sexual selection is false. To make these points, I will describe a view of sexual selection that I consider a consensus view, and use this to consider what should best not be considered sexual selection. First though, I will consider natural selection and why behavioural and evolutionary ecologists choose to go beyond the evolution of fitness to look at individual traits at all.

Natural Selection and Need for Sexual Selection

Evolution by natural selection is driven by competition, be it competition for resources or competition to avoid death, as
ultimately something limits population growth (Darwin 1859). Competition among organisms can take a bewildering array of forms, the identification of which forms the basis of much of modern population ecology. The resulting evolutionary adaptations to competition are themselves equally bewildering, but include some rather satisfyingly paradoxical traits such as cooperative behaviour and the sacrificing of individual reproduction (West et al. 2007). In the end though, all these various forms of competition boil down to competition among individuals in a population to leave the most offspring. If individuals vary genetically in their ability to leave offspring in the face of the biotic and abiotic environment they occur in, natural selection has to result in the genetic change to the population that we think of as evolution (Endler 1986). This is the syllogism at the heart of Darwinian evolution: if individuals differ in their ability to leave offspring, and if these differences are partly heritable, then evolution has to occur.

Evolution by natural selection is therefore a population genetic process. If the Darwinian syllogism holds we will see a relationship form between genotype and fitness. As such, it is not necessary to specify how this relationship forms, that is, to make the links between genotype and phenotype, and then phenotype and fitness, explicit (e.g. Brookfield 2009). Put another way, the only trait that matters for evolution is fitness. However, the population genetic perspective leaves untouched many aspects of organism biology we might care about, in particular the nature of phenotypes. Animal behaviour of course is about all these phenotypes, and from Darwin onwards animal behaviour researchers interested in evolution have used conceptual tools to explore phenotypic evolution. One such tool, often used implicitly, is to try to partition how selection has ‘acted’ on different aspects of the phenotype, including across different stages of an organism’s life cycle. This tool is distinctly Darwinian, in the sense that Darwin himself used it when talking about selection for particular traits (Darwin 1859). In some cases, we have given names to these components of the overall natural selection process, when it has proved useful to focus on certain aspects of phenotypes and consider how selection has acted on them. One of the most influential has of course been sexual selection.

What is Sexual Selection?

Sexual selection describes the selection of traits associated with competition for mates. As such we can say that sexual selection arises from competition for mates (Andersson 1994). To avoid confusion, I define ‘mate’ as a reproductive partner with which one or more zygotes are formed (thereby allowing postcopulatory processes). Despite the work of Roughgarden and colleagues, and indeed the recent commentaries by Carranza (2009) and Clutton-Brock (2009), I consider this to be the standard definition of sexual selection. More formally, sexual selection is the relationship between a trait and its effect on fitness through sexual competition. As such, many traits can be thought of as being both naturally and sexually selected, although from a population genetic viewpoint it is all ‘natural selection’. The debate about the distinctions between natural and sexual selection has a long history (e.g. see Endler 1986; Andersson 1994), but a few words might be useful here. One can view evolution by natural selection in its simplest form if fitness itself is the trait under selection. Components of this process can be identified and considered separately though, which becomes extremely useful when we turn our attention (out of desire or necessity) to the evolution of certain phenotypic traits, rather than just fitness. Such a view is given by Endler (1986) in his Figure 1.2. Sexual selection is then a component of natural selection. Unfortunately, evolutionary biologists then tend to lump all other components of natural selection together and call this ‘natural selection’ (Endler’s ‘nonsexual selection’, or ‘narrow-sense natural selection’), often in the context of viability selection (competition for resources and so on such that an organism lives long enough to engage in competition for mates). For instance, sexual selection is often talked of as being ‘balanced’ by natural selection, as in some models of exaggerated displays or ornaments (Andersson 1994). It probably would be more precise to say that sexual selection may be balanced by other ‘components’ of natural selection, but use of the term natural selection also to mean viability selection is now familiar and well entrenched.

Additionally, Endler (1986) pointed out that statistical descriptions of genetic change derived from the breeder’s equation partition ‘selection’ from ‘heredity’ (i.e. separating selection from genetics). Natural or sexual selection (measured or modelled as selection differentials or gradients) is then no longer synonymous with ‘evolution by natural/sexual selection’. Selection can occur but there will not be genetic change unless there is heritable variation for the trait. As above, this partition has proved very useful (it is the basis of quantitative genetics modelling for example), but it is again a conceptual tool, as nature is not an animal breeder. Consider again the trait of interest to be fitness itself. A term denoting the additive genetic variance in fitness among individuals in fact encapsulates both the necessary genetic variation required for a genetic response and also the defﬁnition of selection itself (fitness differences among individuals), thereby collapsing the partition between selection and heredity, and giving us Fisher’s Fundamental Theorem (Fisher 1930). In this article I will consider sexual selection as a component of an overall natural selection process, and inclusive of both selection and heredity.

Competition for mates can occur in very many forms (Darwin 1871; Andersson 1994), and cooperation between individuals is again not precluded (e.g. DuVal 2007), but it is useful to consider competition over quantity and competition over quality. In terms of quantity of mates, the most basic and familiar form of competition for many of us arises over ‘none’ versus ‘some’. It is well known that in some species some individuals of a given class may fail to obtain a mate because of competition (for instance, male elephant seals and female meerkats: Haley et al. 1994; Clutton-Brock et al. 2006). Alternatively, individuals in a population may for the most part all succeed in finding a reproductive partner, in which case competition may become focused on the quality of that partner. If certain individuals represent a better reproductive resource (there will be a greater number of offspring produced by that partner), it is clear that competition can arise for access to those individuals as reproductive partners, as it can in any other ecological context. How those partners are obtained may vary, from out and out coercion (Clutton-Brock & Parker 1995) to taking advantage of being a limited resource and choosing only to mate with the most appropriate partner(s) (Bateson 1983). It is for this reason that sexual selection is not precluded in strictly monogamous species (Darwin 1871), and mutual mate choice where both members of reproductive pairs make mate choices is now well established (Kraaijeveld et al. 2007; Clutton-Brock 2009). For sexual selection not to occur in a population, there either has to be no scope for competition (partners as resources are not limiting, and all partners are of equal quality), or the outcome of any competition for mates is totally random with respect to the traits expressed by individuals, such that successful partnerships represent a random sample of pairs of individual phenotypes (and thus genotypes). While we cannot claim that competition for reproductive partners, and thus sexual selection, is ubiquitous (and as Roughgarden & Akçay 2010 note, not all sexual selection processes act in all populations at all times), it has been abundantly clear since Darwin that sexual selection describes something that commonly occurs in nature, with effects that are nontrivial at the phenotypic level. And to make
this point extremely clear, for sexual selection to be ‘wrong’ and not to occur at all (as suggested by Roughgarden et al. 2006), we have to show that one or both of the premises of the syllogism underlying sexual selection are always untrue in natural populations. As such, either there would never be variation among individuals in their success at obtaining (potentially high-quality) mates, and/or there would never be additive genetic variation among individuals in traits that influence this success. Male guppies have pigmentation that influences their success in mate competition. Male guppies have heritable differences in pigmentation. There is sexual selection in guppies (Brooks & Endler 2001). One could go on, but I hope it is sufficient just to note here that, like its twin sister natural selection, sexual selection happens (Andersson 1994).

Viewing sexual selection as competition for mates is to define sexual selection in broad terms. In their commentary in response to Clutton-Brock (2009), Roughgarden & Akçay (2010) suggest that any such broad definition of sexual selection is ‘devoid of any specific meaning’. I find this unconvincing, not least because natural selection, which is of course a description of an overall process that is even broader and subsumes all forms of competition among organisms for future genetic representation, seems to have both a pretty clear meaning and great intellectual utility. Why sexual selection should then be singled out for being overly broad is not clear. If we look for similar examples in ecology, do we find that the concept of density dependence is too broad and therefore meaningless because of the almost innumerable ways in which it can be manifested? Sexual selection, like density dependence, may encompass a lot of processes but the logic at its heart is simple and the premises refutable.

Other definitions of sexual selection have made attempts to make explicit just what it is that is being competed over, including fecundity and resource acquisition that increases fecundity (see Clutton-Brock 2007, 2009). Fecundity (which entails how energy to be invested in reproduction is spread among ova) may be both naturally and sexually selected from a phenotypic point of view. In terms of sexual selection, fecundity may be selected if by being more fecund one attracts an individual who is a better reproductive partner in some way. Such sexual selection may of course in turn increase the competition for mate quality (highly fecund partners). However, fecundity can be fixed in a population and sexual selection still act. In contrast to Clutton-Brock (2007, 2009), I would argue that fecundity by itself, when not associated with competition for mates, is best considered as only being naturally selected (even if it leads to sexual dimorphism). Otherwise sexual selection comes to equate itself with natural selection. Clutton-Brock (2009) considered female–female competition for resources as a possible candidate for a sexual selection process, but going down this route of course means that all foraging behaviours (and indeed all behaviours that mean an individual does not die before managing to become reproductively mature) become associated with differences in fecundity (or sperm load say, if we switch attention to males). At this point, the benefit of a conceptual tool that partitions (and names for convenience) different aspects of the population genetic natural selection process becomes moot, and we might as well revert to just thinking about natural selection, a point made by Clutton-Brock (2009). I do not think we need to go that far though. Viewing sexual selection as competition for mates, while general in the sense of covering a wonderfully diverse range of phenotypes, is actually an excellent focus for researchers: is there competition for mates, and does a given trait influence that competition? If a trait does not, then there are plenty of other drivers of ecological competition (for resources, enemy-free space and so on) that may have left their evolutionary mark on a trait.

Although competition for mates can occur in many different contexts (Andersson 1994), some have received rather little attention from behavioural ecologists (a point also made by Clutton-Brock 2009). That lack of attention is historical and it does not in itself represent a statement of what sexual selection ‘is’. For example, sexual selection can occur in isogamous species (e.g. Rogers & Greig 2009) even though the seminal monograph of Andersson (1994) is not full of such examples. In a similar vein, both isogamous and anisogamous gametes can compete for reproductive partners in order to create a zygote. In this case, the quantity of partners for a gamete over which competition arises is (usually) zero or one. Gametes may also vary in quality (for instance in terms of resources provided by the parent) and gametes of the complementary sort may compete for access to each other. The role of sexual competition in gamete evolution is now well established (Birkhead et al. 2009).

Competition for mates has the potential to arise among all classes of organisms in a population, and Darwin (1871) famously pointed out the two forms it would take: intraclass competition and interclass choice, where ‘choice’ refers to aspects of the phenotype that bias the probability that an individual of one class will become the reproductive partner of an individual of the other class (as such, ‘choice’ may sometimes seem an unfortunate term). In terms of isogamous species, there may therefore be intramating type competition (intermating type choice). In terms of anisogamous gametes, we can envisage intramating-type competition (among sperms and among ova) and intergamete choice (including passive attraction to gametes of certain phenotypes, or by making fertilization for one class of gamete difficult for the other class). However, it is in anisogamous species at the organismal level, with sperm-producing male tissues and ova-bearing female tissues, that sexual selection has been most thoroughly conceptualized and studied.

**How Controversial is this View of Sexual Selection?**

The extent to which this view of sexual selection is controversial will be in part measured by the number of readers that have already got bored and stopped reading. My perception is that the above represents the consensus among evolutionary biologists of what sexual selection is (and is at the heart of the view of sexual selection given by Andersson 1994). But clearly controversy is in the air. Of course, researchers can call whatever they like sexual selection, but in doing so a clear conceptual framework is needed. I contend that we already have one, and that the ‘conceptual malaise’ identified by Roughgarden & Akçay (2010) will come as a big surprise to the vast majority of evolutionary biologists. Using the above framework, I will suggest some things that should not be called sexual selection or confused with sexual selection, highlighting where possible the conceptual consequences of ignoring these suggestions.

**What Sexual Selection Should Not Be**

Sexual selection should not be a description of the difference in how selection has acted on males and females (as suggested by Carranza 2009). While that phenomenon is currently of great interest, and likely to be pervasive in nature, we already consider it sufficiently under the umbrella of sexually antagonistic selection and sexual conflict (Chapman et al. 2003; Arnqvist & Rowe 2005). A difference in selection on traits in males and females (or the influence of sex on selection, to paraphrase Carranza) is not Darwinian sexual selection, not least because these differences may be unrelated to reproduction (ecological selection on dimorphism for example: Shine 1989), and this means that what Carranza would call sexual selection might influence traits not associated with reproduction. This seems a long way from how sexual selection is currently used. Moreover, the fact that isogamous organisms...
with sexual reproduction, but no ‘sexes’, can experience sexual selection pretty much seals the case. I therefore concur with Roughgarden & Akçay (2010) that the attempt by Carranza to change the definition of sexual selection is less helpful than it might be. Of course, sexual selection as currently understood may well have contributed to traits having different fitness effects in males and females, but turning the logic around is problematic.

Sexual selection is also not just intersexual choice, let alone just female choice. As already explained, intra- and interclass processes co-occur within the framework of sexual selection. It seems of little conceptual relevance to use sexual selection exclusively to refer to one aspect of competition for mates, whether or not a topic such as phenotype, all selection would stop on them as well. Thus intra-sexual selection in the next generation all the males displayed the preferred phenotype, all selection would stop on them as well. Thus intra- and interclass selection together to reproduce, and what opportunities there are for selection. For example, all sorts of aspects of mating systems theory seeks to address why particular mating (or class can sometimes be competitive, and sometimes choosy, all females made the same choice, there would be no variation in selection. For example, all sorts of aspects of mating systems theory takes the biology of an organism (from its physiology, through to its life history and ecological analogies with respect to natural selection abound. Perhaps most importantly, sexual selection is not dependent on what have been termed ‘sex roles’ (who chooses, who competes and so on). This is clear from again considering competition for reproductive partners in organisms without sexes, and is also abundantly clear from the many natural systems where both sexes engage in mate choice (Kraaijeveld et al. 2007). It is true that Darwin (1871) did notbelabour this point, and that most of his writing on sexual selection proscribed male and female sex roles in a rather ‘traditional’ way (most, but not all: see below). It is also true that behavioural ecologists may seem to drop by default into assuming that sexual selection comprises ‘male–male competition’ and ‘female choice’. However, one really does not have to go very far to appreciate that behavioural ecologists have not actually been that stupid (reading Andersson 1994 will suffice). One of the most curious aspects of the challenge to sexual selection put forward by Roughgarden and colleagues has been their contention that the existence of ‘sex role-reversed’ species are in some way fatal to sexual selection. Rather, such species have long been taken to support our ideas of how mating systems work and evolve, especially when we manipulate ‘sex role’ by manipulating which sex is the more limiting (e.g. Gwynne & Simmons 1990; Simmons & Bailey 1990; Simmons 1992). The fact that individuals of a given class can sometimes be competitive, and sometimes choosy, all
depending on how different aspects of the environment and species’ biology influence competition for mates as a whole, fits mating systems theory rather nicely. The problem is we do not yet have all the answers. This may be simply because aspects of a species’ biology and ecology that would allow us to make better predictions are poorly known for all but a few species. In any case though, our ability to understand and predict the causation of sexual roles is the purview of mating systems theory; sexual selection does not need males or females to have one sex role or another, it just needs competition for mates.

Sexual selection is not the same thing as sexual conflict. The shift in the way we have viewed reproductive interactions over the last century or so has been well documented (e.g. the well-known change in moral status of the dunnock: Davies 1992; Arnqvist & Rowe 2005). This reinterpretation continues, as it should, to this day. Over the last 15 years or so, driven by empirical observations (most notably in insects), the idea of conflict between males and females over reproductive decisions has become a dominant theme (Arnqvist & Rowe 2005). While it is clear that males and females have to cooperate to some extent in order to mate, especially in internally fertilizing species, both theory and (to a lesser extent) experiment have moved us to view the context in which reproductive behaviour evolves as one primarily driven by sexual conflict rather than sexual cooperation. The key of course is the phrase ‘to some extent’. In some insect species, male–female reproductive interactions may be brief, with much of the interaction dominated by a mating struggle as males try to force mating (as in seaweed flies or water striders: Rowe et al. 1994; Shuker & Day 2001). In these species, ‘to some extent’ is not very much. In many other taxa, on the other hand, such as socially monogamous birds, reproductive interactions include significant investment in parental care by both parents, male and female alike (reviewed in Clutton-Brock 1991). In these cases, ‘to some extent’ may actually be quite a lot.

That said, behavioural ecologists will probably need to continue to explore the relationship between sexual selection and sexual conflict. For instance, given the current re-emergence of the ‘good genes’ sexual selection debate (as mentioned by Roughgarden & Akçay, 2010) and some of the important structural weaknesses underlying existing models of intersexual choice (outlined by Arnqvist & Rowe 2005), there is a current enthusiasm for sexual conflict models of the evolution of mate preferences (Holland & Rice 1998; Gavrilets et al. 2001; Cameron et al. 2003). In these models, mate preferences (behaviours that bias the mating success of the opposite sex) are in fact the outcome of attempts to limit (implicitly) costly mating interactions, thus ‘choosing’ individuals that are able to overcome or subvert those attempts (but this is still sexual selection, only ‘chase-away’ sexual selection in terms of competition among the ‘choosy’ sex to limit matings to the minimum necessary: Holland & Rice 1998). These models are attractive and have rightfully received a lot of attention (although not necessarily in terms of experimental tests). However, the fact that a sexual conflict over mating can lead to sexual selection does not mean that sexual conflict is sexual selection (or vice versa). The two are definitely at risk of being conflated by the unwary though.

Sexual Reproduction as a Cooperative Venture

One of the main criticisms voiced by Roughgarden & Akçay, in the current article and others, is that the emphasis on sexual competition and conflict fundamentally misunderstands how evolution has shaped reproductive behaviour in animals. Part of this critique is motivated by the use of certain game-theoretical tools, and in particular the impact of the work of Maynard Smith (1982). Their main contention is that evolutionary game theory has been developed from only one strand of game theory as originally developed by economists such as Nash (Roughgarden & Akçay, 2010). In particular, they argue that Maynard Smith introduced ‘competitive’ game theory to biology, but failed to introduce ‘cooperative’ game theory, which is based on between-actor negotiations (although this interpretation of what constitute different strands of game theory is contested: e.g. Dall et al. 2006).

At one level it might not seem a particularly important point, not least because much of the sexual selection theory developed (especially in terms of mate choice) has been avowedly population genetic in nature (Kokko et al. 2006). However, clearly game theory, in the guise of evolutionarily stable strategies (ESSs), has penetrated the psyche of behavioural ecology. Has it done so to the detriment of our understanding of sexual selection? I suggest not for three reasons. First, game-theoretical models in behavioural ecology have actually developed over the years to consider behavioural negotiation (e.g. Houston et al. 2005; Johnstone & Hinde 2006). These models generated useful predictions and did so without creating a crisis in evolutionary ecology. Second, much of the context given for this alternative modelling framework sits firmly in the field of the evolution of parental care, not sexual selection at all. Parental care, or more generally the patterns of parental investment within and among the sexes, has been an important component of mating systems theory, from Trivers (1972) onwards. However, parental investment need have no a priori link to the pattern of sexual selection since a whole array of ecological factors may influence how individuals of a class compete for mates (see above). Third, a rigorous critique of sexual selection that calls for a major redefining of what we mean by sexual selection and how we model it surely needs to be one that is broadly applicable across taxa. As an insect behavioural ecologist, it is not at all clear to me how the inclusion of behavioural negotiations in some form of new sexual selection theory could have anything other than a marginal impact on most reproductive interactions in insects. Of course, one could frame any interaction in terms of a ‘negotiation’ if one wanted, but it is not clear this would be much more than a semantic gesture in many cases. I could repeatedly punch someone and say it was a negotiation, but members of the local constabulary may consider the interaction less than harmonious. Is it really helpful therefore to reimagine vigorous mating struggles and acts that look like rejection behaviour as ‘negotiations’ (Rowe et al. 1994)? The same of course is likely to be true for sexual selection in plants, if one wishes to look outside animals.

Perhaps the most important point to remember though, which is in fact implicit in the work of Roughgarden and colleagues, is that behavioural negotiations do not ‘remove’ conflict from mating interactions, because they could only exist and be relevant if there is conflict present in the first place. Rather, negotiations may provide a strategy to ameliorate the expression of conflict, and ‘resolve’ it even, such that cooperative outcomes result. These outcomes will only arise though if cooperation, be it reached via real-time negotiation or as part of a genetically programmed behavioural repertoire, has a higher inclusive fitness. Organisms will not negotiate just to be ‘nice’. In summary, the behavioural tier introduced by Roughgarden and colleagues may prove useful in certain circumstances, but these models cannot redefine sexual selection.

What did Darwin Think?

One aspect of the sustained critique of sexual selection by Roughgarden and colleagues has been that various societal biases associated with gender have detrimentally influenced how scientists have thought about sexual selection. Moreover, it is argued...
that this goes right back to Charles Darwin himself (e.g. Rough-garden 2007). The problem of what Darwin really meant has also cropped up in the recent commentaries by Carranza (2009) and Clutton-Brock (2009). One could easily devote many pages to this, but here are two points perhaps worth briefly considering. First, of course scientific interpretations are not immune from the societies in which they are made (sexual selection provides a nice case study after all: Cronin 1992). What matters though is how enlightening those interpretations remain in the face of new data and new interpretations. The fact we are still all thinking about sexual selection is testament to the lasting value of Darwin’s insight, even if we may wish he had left us with a clearer sound-bite of a definition. Second, just what did Darwin think? The answer depends on where you look. In their recent biography, Desmond & Moore (2009) detail how Darwin’s thoughts on sexual selection developed over time (especially in terms of its relationship with human evolution), and that development was not straightforward. For instance, in a notebook from 1837 Darwin was able to make notes on female–female competition for males (Desmond & Moore 2009), a long way from the classic view of Darwin and his coy, choosy females ‘selecting... males, according to their standard of beauty’ (Darwin 1859). And similarly, while The Descent of Man (Darwin 1871) is undoubtedly home to much of what we now would consider gender-role stereotyping he was also able to assert that sexual selection ‘depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction’, a definition notably devoid of explicit gender roles. However, with thoughts developing nonlinearly over time, coupled with the (very frustrating!) 19th Century practice of making often substantial revisions to books for new editions across many years, trying to ascribe to Darwin a definitive view of sexual selection must ultimately be somewhat unsatisfactory (as indeed it would be for anyone; see Reeves 2007 for a similar discussion of attempts to claim the thought processes of Darwin’s equally brilliant contemporary John Stuart Mill). Thus, trying to say whether Darwin got it right or wrong on sexual selection is a bit like trying to claim Darwin for religion or atheism: you pay your money and take your choice (of quotations).

Do We Need a New Sexual Selection?

Do we need sexual selection version 2.0? Given the fall and rise of the popularity of intersexual selection since Darwin (Andersson 1994), the discovery of postcopulatory sexual selection (Parker 1970; Eberhard 1996), the change in our understanding of the role females more typically play in mating systems (Reynolds 1996; Clutton-Brock 2009), and a broader appreciation of sexual conflict (Arnvist & Rowe 2005), it is clear that we are already well past version 2.0. But do we need a fundamental redefining of sexual selection? I argue not. All of these discoveries change our understanding of what Darwin really meant has also cropped up in the recent commentaries by Carranza (2009) and Clutton-Brock (2009). One could easily devote many pages to this, but here are two points perhaps worth briefly considering. First, of course scientific interpretations are not immune from the societies in which they are made (sexual selection provides a nice case study after all: Cronin 1992). What matters though is how enlightening those interpretations remain in the face of new data and new interpretations. The fact we are still all thinking about sexual selection is testament to the lasting value of Darwin’s insight, even if we may wish he had left us with a clearer sound-bite of a definition. Second, just what did Darwin think? The answer depends on where you look. In their recent biography, Desmond & Moore (2009) detail how Darwin’s thoughts on sexual selection developed over time (especially in terms of its relationship with human evolution), and that development was not straightforward. For instance, in a notebook from 1837 Darwin was able to make notes on female–female competition for males (Desmond & Moore 2009), a long way from the classic view of Darwin and his coy, choosy females ‘selecting... males, according to their standard of beauty’ (Darwin 1859). And similarly, while The Descent of Man (Darwin 1871) is undoubtedly home to much of what we now would consider gender-role stereotyping he was also able to assert that sexual selection ‘depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction’, a definition notably devoid of explicit gender roles. However, with thoughts developing nonlinearly over time, coupled with the (very frustrating!) 19th Century practice of making often substantial revisions to books for new editions across many years, trying to ascribe to Darwin a definitive view of sexual selection must ultimately be somewhat unsatisfactory (as indeed it would be for anyone; see Reeves 2007 for a similar discussion of attempts to claim the thought processes of Darwin’s equally brilliant contemporary John Stuart Mill). Thus, trying to say whether Darwin got it right or wrong on sexual selection is a bit like trying to claim Darwin for religion or atheism: you pay your money and take your choice (of quotations).

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Forum

Final response: sexual selection needs an alternative

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Shuker (in this issue) enumerates five points and we organize our response accordingly.

First, we agree that sexual selection (and social selection) are subsets of natural selection, and therefore share the same logical framework of natural selection. We do not agree that natural selection is ‘driven by competition, be it competition for resources or competition to avoid death, as ultimately something limits population growth’. It is true that in Chapter 3 of \textit{The Origin of Species}, Darwin (1859) wrote of natural selection as a struggle for existence caused by resource limitation, as ‘the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms’ (page 63), and wrote, ‘There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair’ (page 64). This framing of natural selection as resulting from resource competition was superseded by the neo-Darwinian formulation of early population genetics in which fitness is understood as the product of fertility with survival. Conferring a higher fitness by this definition is sufficient for a gene to fix in the gene pool without reference to competition for resources. A higher fitness could be attained with higher efficiency under unlimited resources.

To say that natural selection is always driven by competition widens the meaning of competition beyond common usage in ecology. For example, the colonization phase of community succession, which lacks competition, is distinguished from the climax phase in which competition occurs. Similarly, the \( r \)-selection phase of population dynamics during density-dependent evolution involves natural selection for efficiency and productivity whereas the \( K \)-selection phase involves natural selection resulting from competition. To be sure, evolutionary writers sometimes view all natural selection as resulting from competition regardless of whether resources are limiting. Bell (2008, page 15), for example, refers to ‘competition’ as occurring when ‘variants with greater exponential growth rates are selected’ during density-independent population growth (i.e. during \( r \)-selection), saying that ‘the nature of competition changes’ when the population dynamics transition from density-independent selection to density-dependent selection (i.e. from \( r \)-selection to \( K \)-selection). We do not consider \( r \)-selection, that is, differential density-independent growth, as

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'competition'. If competition and natural selection are synonymized, saying that competition ‘drives’ natural selection is empirically meaningless because this is then true by definition and could not be falsified, and moreover imparts the ideological connotation that competition enjoys a logical priority and universality in biological evolution. Instead, competition for resources, that is, crowding in the original Darwinian and Malthusian sense, is merely one of many mechanisms that can cause natural selection, and it is not always present. Even though natural selection is indeed ubiquitous, it does not follow that competition is ubiquitous too, and in particular, it does not follow that competition for mates is ubiquitous either.

Second, we agree that what Shuker terms ‘mating systems theory’ is not the same as sexual selection itself. We recognize a distinction between core and peripheral issues pertaining to sexual selection by referring to a ‘central narrative’ within the sexual selection ‘system’ of theories. Our terminology draws attention to the logical connections among these theories. Mating systems theories expand upon the sexual selection narrative and sexual selection theory relies on mating systems theory to make concrete predictions. Take, for example, extrapair copulation (EPC). By any definition of core sexual selection, the explanation of EPCs lies beyond the core. If one views the core of sexual selection as being about females selecting males for good genes, then EPCs follow logically as a tactic for females to secure a genetic upgrade over their pair male. So, failure to confirm that extrapair males have better genes than pair males reflects back on the truth of the core sexual selection that was the premise from which this particular EPC theory was derived. Such a failure to confirm would at least provoke a restatement of what can be derived from the core specifically concerning EPC, and if many such theories were found to be unconfirmed, a reexamination of the truth of core sexual selection. The point is, any definition of core sexual selection is logically connected to the peripheral theories pertaining to it, including all of mating systems theory as well as many other issues such as the evolution of anisogamy (cf. Roughgarden 2009, Table 19, pp. 237–238), all of which unite as one of evolutionary biology’s master narratives. Thus, sexual selection and mating systems theory are logically interdependent, and falsifying either of these components within the sexual selection system has repercussions for the other components.

Shuker defines core sexual selection as ‘the selection of traits associated with competition for mates’. Moreover, he defines a mate as ‘a reproductive partner with which one or more zygotes are formed’ thereby ruling out the ample variety of known same-sex matings, even though same-sex matings might carry out the same social functions as between-sex matings. This definition allows that much sexual activity, both hetero- and homosexual is not about mating, and is not part of mating systems theory, but of some other topic, such as the emerging subject area of animal friendships. Moreover, as stated, Shuker’s definition refers solely to behaviour. However, Shuker also requires that the traits involved must be heritable, and Shuker describes ‘sexual selection as a component of an overall natural selection process, and inclusive of both selection and heredity’. We agree that sexual selection pertains to behaviour with evolutionary consequence, and not to the behavioural act of mate selection itself.

Shuker considers that his definition of sexual selection ‘represents the consensus among evolutionary biologists of what sexual selection is’. We think this perception of consensus requires careful picking of the sample population. In our experience, most biologists, including evolutionary biologists, together with present and former biology students, not to mention social scientists such as evolutionary psychologists and anthropologists, think of a specific narrative when queried about what sexual selection is. They think of males fighting with one another for access to and/or control of females, of females choosing males whose good genes are revealed though displays, ornaments or armaments, and of an evolutionary rationale for such behaviours that traces to sperm being cheap and eggs expensive. Most biologists are then surprised to hear that this archetypal narrative may often be incorrect, and they are especially surprised when an archetypal example such as the peacock needs reinterpretation. Shuker relegates this archetypal sexual selection narrative to the domain of ‘mating systems theory’, many parts of which Shuker allows ‘could be wrong’ and which he also acknowledges show a ‘lack of experimental work’. He states further that, ‘clearly our grasp of mating systems is not as complete as we perhaps thought’. But relocating the archetypal narrative of sexual selection to mating systems theory so that its failure can be dismissed as having ‘no effect at all on the logical basis of sexual selection’ is evasive, or as Shuker himself recognizes, very ‘convenient’. If one is serious about placing mating systems theory, including the archetypal narrative of sexual selection, at arms length from ‘core’ sexual selection, then textbook writers and other decision makers who influence biology curricula worldwide should be informed so that the present widely taught accounts of sexual selection can be revised.

We do not feel strongly about how sexual selection is defined, provided that the definition allows sexual selection to be falsified with data and acknowledges that alternatives exist. We object when the definition is slippery, infinitely malleable, and continually revised in light of contrary data, making the theory unfalsifiable. In our own work, we typically employ a definition of the ‘central narrative’ that is closer to Darwin’s original statement than is Shuker’s definition, namely, that sexual selection is ‘Natural selection from differences in mating success. Males compete for mating opportunities, females are a ‘limiting resource’ for males, and females choose males for genes’ (Roughgarden, 2009, Table 1, page 62). We argue that sexual selection in this sense does not occur, and we accept Shuker’s observation that ‘the criticisms of Roughgarden and colleagues lead more to mating systems theory than they do to sexual selection per se’, according to his definition. In this light, the reservations Shuker has expressed about the correctness of present-day mating systems theory are an important concession. Still, for the present exchange we are happy to work with Shuker’s broad definition of sexual selection, namely, as any selection resulting from competition for mates, which we do accept as concrete and falsifiable. However, by this definition too, the evidence for sexual selection is weak, as discussed further in point five below.

Third, we disagree with the claim that ‘the action of sexual selection is unaffected by whether the behavioural interactions between mating partners during reproductive episodes are considered cooperative or selfish’. By the letter of Shuker’s own definition of sexual selection, namely selection associated with competition for mates, if the interactions between potential or actual mates are anything other than competitive, say cooperative, then manifestly, sexual selection is not taking place.

Still, the text of Shuker’s comment dwells on what he feels is the importance of competitive game theory in behavioural ecology and the sufficiency of Maynard Smith’s (1982) evolutionarily stable strategy (ESS) concept in particular. He also remarks that our alternative modelling framework pertains to ‘the evolution of parental care, not sexual selection at all’, and as such is banished to the hinterland of mating systems theory.

We suspect the discussion here is at crossed purposes. Our position is that sexual selection theory misconceptualizes the reproductive process. Sexual selection focuses entirely on mating, both the act of mating and the identity of the mating partner, and relegates what happens next to a distinct topic of ‘parental care’. Please cite this article in press as: Roughgarden, J., Akçay, E., Final response: sexual selection needs an alternative, Animal Behaviour (2010), doi:10.1016/j.anbehav.2009.12.029
Instead, we focus on the integrated and indivisible social process that yields offspring who are counted in the next generation. Mating is an instrumental part of this process, perhaps not so much because of the exchange of gametes, but because of the social bonds that mating and other affiliative behaviour produces. In the social selection perspective, courtship and mating behaviour are part of an extended view of how parental and social investments are allocated. And a reproductive social group, from a monogamous pair to an extended family, is a ‘firm’ whose product is offspring.

We have further argued that a theory of social selection must depart from the game-theoretical framing introduced by Maynard Smith (1982) because we need to introduce a wider variety of game-theoretical solution concepts than that corresponding to the ESS because we think the ESS is not sufficient. We feel the most convenient taxonomy of solution concepts distinguishes what we have termed cooperative game theory from cooperative game theory, as illustrated by the distinction between playing chess where the players cannot communicate and playing monopoly where the players can communicate to make deals. We do not deny that others might prefer other taxonomies. All in all, we advocate the wider use of game theory.

One of the new solution concepts that seems interesting with respect to intimate familial friendships, including both within- and between-sex pair bonds, is the Nash bargaining solution (NBS). None the less, we freely use competitive solution concepts as appropriate. For example, we envision parents who, as ‘owners’ of a firm (or ‘conglomerate’, Groves 1973) that produces offspring, set incentives for offspring participation as helpers in the group’s reproductive activity: an approach consistent with, and synthesizing, Alexander’s (1974) view of parental control, Vehrencamp’s (1983) concept of staying incentive, as well as extensions to skew theory such as social queuing (Kokko & Johnstone 1999) and parental imposition of costs (Crespi & Ragsdale 2000). The offspring serve as members of their parent’s reproductive firm because each maximizes its own fitness by doing so, which represents a noncooperative solution, given that the parent can set the incentive structure. Accomplishing the introduction of a wider array of solution concepts requires splitting the modelling into two tiers, as compared with the original single population-genetic tier formulation of Maynard Smith because these other solution concepts do not arise in gene-pool dynamics.

We have stated many times that an apparently cooperative outcome can indeed be achieved with solely competitive dynamics, as illustrated by the division of space into territories through competitive engagements between neighbours (e.g. Roughgarden 2009, pp. 151–154). But are all cooperative outcomes the result of competitive dynamics? Animal friendships, and the evolution of other-regarding preferences, raise the possibility that cooperative outcomes can also be realized through cooperative means. We have proposed the NBS as a possible criterion to predict the outcome of a cooperative path to a cooperative end. And we can only take advantage of an extended set of solution concepts when we consider the possibility that social-behavioural dynamics do not march in lock step with gene-pool dynamics because these are governed solely by the ESS.

We respect that insect ecologists find animal negotiations more implausible for insects than, say, for vertebrates. Still, many have witnessed intimate contact between insects, and we are not aware that the possibility of friendships has been investigated in insects, especially today, when sexual conflict is so much in vogue.

Fourth, we agree that whether sexual selection exists ‘does not depend on what roles’ the different reproductive classes (mating types or sexes) take during reproductive interactions’, assuming, that is, that sexual selection is defined solely as competition for mates. The question of who competes for whom is then relegated to ‘mating systems theory’. Hence, sex role-reversed species are now, by fiat, no longer problematic for sexual selection itself, because either sex can do anything and still count as sexual selection so long as competition for mates is taking place. But, as Shuker notes, Darwin (1871) prescribed male and female sex roles in a ‘traditional’ way, as near-universal generalizations (‘with the rarest of exceptions’). Shuker notes too that ‘behavioural ecologists may seem to drop by default into assuming that sexual selection comprises ‘male–female competition’ and ‘female choice’, although the cognoscenti are assumed never to commit this ‘stupid’ error, to quote Shuker’s adjective. Still, many leaders in behavioural ecology, now and in the past, continually adopt the cheap-sperm/expensive-egg narrative as integral to sexual selection, as even a contributor to this Forum exchange illustrates.

The step from assuming that sperm are cheap and eggs expensive to concluding that males are naturally promiscuous and females naturally choosy is quickly taken, inviting the hasty dismissal of copious exceptions. Although a solely competition-for-mates definition of sexual selection is not challenged by sex role-reversed species, the many narratives that incorporate the cheap-sperm/expensive-egg premise are challenged. In sex role-reversed pipefish, males make sperm each of which is much smaller than an egg, and often they provide the parental care, and may therefore be in the better bargaining position relative to females who are seeking partners to care for their eggs. Thus, gamete size does not predict or explain sex role. Therefore, even if sexual selection is defined to remain intact in the face of sex role-reversed species, a central tenet of commonly taught sexual selection narratives is false, and, instead, one cannot derive sex role from gamete size. We would applaud any systematic effort to publicize the disconnect between sexual selection and sex roles, so that even if sexual selection does turn out to occur, it cannot be used to naturalize traditional sex roles, which brings us to the last point.

Fifth, we disagree that compelling evidence presently exists for sexual selection in nature. We accept that sufficient (although not necessary) conditions for sexual selection not to occur in a population are (1) that ‘all partners are of equal [genetic] quality’, or (2) that the outcome of mate selection is that ‘successful partnerships represent a random sample of pairs of individual phenotypes (and thus genotypes)’. By these very criteria, the existing empirical case for sexual selection is lacking.

The paradox of the lek pertains precisely to the question of whether all partners are of equal genetic quality. In the absence of an external source to resupply continually the bad genes in males that female choice is supposedly pruning every generation, all males wind up genetically equal in fitness, thereby defeating the value of continued female choice. Although untested proposals exist for mechanisms that might generate an endless supply of bad genes to merit making it worthwhile for females to continue screening males for genetic quality, the evidence argues that males are in fact of equal genetic quality. The 24-year collared flycatcher study on Gotland Island in Sweden by Qvarnström et al. (2006) shows exactly what is expected if the paradox of the lek is indeed true. Fitness differences between male collared flycatchers are not inheritable, even though the badge size is inheritable, so it is a waste of time for females to bother selecting males on the basis of badges in hopes of endowing their sons with fitness-enhancing good genes. And these investigators in fact found that female choice for badge size had nothing to do with genetic quality. Hence there is no sexual selection in collared flycatchers by Shuker’s criterion.

Instead, Shuker offers the interesting study on male guppies by Brooks & Endler (2001) as a clear-cut case establishing the reality of sexual selection: ‘Male guppies have pigmentation that influences their success in mate competition. Male guppies have inheritable differences in pigmentation. [Therefore,] There is sexual selection
in guppies'. QED? Invoking this 'Darwinian syllogism' would seem to settle the matter. But is mating success the same as fitness, in nature or the laboratory? Do the attractively ornamented males in nature reliably leave more offspring in the next generation than the unattractive males, thereby offering grounds for females to choose attractive males as mates to acquire their good genes? If not, then sexual selection is absent by Shuker's criterion. Brooks & Endler present data solely on attractiveness and mating success in the laboratory, not on fitness itself in natural populations. So we do not know whether the ornamented males differ in genetic fitness from the unornamented males. Compare with the collared flycatcher case. In this species too, the background information seemed clearly to implicate sexual selection in maintaining the male ornament. Yet, sexual selection was absent, after all. The male guppy case, while possibly offering an example of sexual selection, is not conclusive, and the continuing failure of sexual selection's other poster-child species to withstand scrutiny invites scepticism here too.

It has been argued to us that 'whether or not attractive males have high fitness in terms of fitness components outside of reproductive competition can be irrelevant to the action of sexual selection'. No. According to sexual selection, female choice is supposed to use the ornament to identify males who have genes she should endow her sons. If some genes promote mating success at a cost to other fitness components resulting in no net fitness advantage, then seeking out such males as mates is pointless. A marker for those genes should be selectively neutral.

Shuker also mentions the interesting recent study by Rogers & Greig (2009) of mate competition in yeast, an isogamous species. These investigators set up an experimental scheme in the laboratory whereby a gene conferring success in mate competition could evolve to fixation. Yet the authors clearly discuss morphological and cellular mechanisms that minimize sexual selection in nature, and their innovative experimental set-up circumvents these obstacles. Although the experimental set-up that results is likely to be a valuable tool to test evolutionary hypotheses, the evidence for sexual selection in nature remains inconclusive.

Shuker's second criterion for the absence of sexual selection is that successful partnerships represent a random sample of genetic pairings. This situation results when the bad genes consist of accumulated weakly deleterious mutations. Byers & Waits (2006) assert that mating behaviour in pronghorn antelopes demonstrates selection for good genes because female choice of male prowess supposedly weeds out males who have accumulated a load of weakly deleterious mutations. But the fitness difference between a genetically good male and a genetically bad male is less than 1%, according to population-genetic theory for how weakly deleterious genes accumulate. (cf. Roughgarden 2009, pp. 51–54.) This difference is surely undetectable by females in any conceivable natural setting. Therefore, mating pairs of antelopes probably represent random pairings with respect to their genetic quality, rendering sexual selection absent according to Shuker's second criterion. Byers & Waits's conclusion which states, in effect, that sexual selection endows all species with a natural system of eugenics to weed out bad genes is unwarranted by the evidence they supply.

In conclusion, Shuker asks why sexual selection should be 'singly out for being overly broad'? He writes, 'If we look for similar examples in ecology, do we find that the concept of density dependence is too broad and therefore meaningless because of the almost innumerable ways in which it can be manifested? Sexual selection, like density dependence, may encompass a lot of processes but the logic is simple and its premises are refutable. We single out sexual selection because it is logically central to an entire system of explanation for animal social behaviour. Challenging dubious specifics within what Shuker terms 'mating systems theory' is useless when the specifics all claim to derive their legitimacy from the narratives of sexual selection. Getting the explanations of social behaviour right inevitably requires determining whether sexual selection itself is true: always, often, rarely or never.

The comparison with density dependence is instructive. Ecologists do not assume that density dependence inevitably exists. They once did, but not now. During the 1950s and later, Andrewartha & Birch (1954, cf. Ehrlich & Birch 1967) explored mechanisms for the density-independent persistence of a population. Now, for anyone studying population regulation, a necessary first step is to reject a density-independent null hypothesis, prior to fitting a density-dependent model such as a logistic or Ricker equation. Alternatively, a population might in fact not possess any effective density dependence, such as marine populations with no detectable stock recruitment relation or butterfly populations whose abundance always remains too low to effect defoliation and whose annual fluctuations in abundance depend on diapause rates controlled only by the timing of the winter's final rainfall. Similarly, community ecology in the 1980s saw the beginnings of 'neutral theory' (Hubbell & Foster 1986; cf. Hubbell 2001) that has been effective in accounting for community patterns in Panamanian rainforest as an alternative to the earlier 'community matrix' species-interactive view of community structure from MacArthur & Levins (1967) and Hutchinson (1959). And even natural selection has genetic drift as its principal alternative hypothesis.

What about sexual selection? Where is the alternative? A null model for the reproductive skew expected by a Poisson process of mate selection has been presented by Sutherland (1985) and Hubbell & Johnson (1987). By and large though, no extensive alternative hypothesis exists for sexual selection that potentially matches its scope ranging from core sexual selection through its derivative mating systems theories. Sexual selection needs to be tested against a fully fledged alternative before it can be accepted as having been demonstrated. We anticipate that sexual selection cannot withstand such a test based on our reading of the evidence so far. For those who already accept sexual selection, the available data seem to fall nicely into place, whereas through the eyes of those who still need to be convinced, the case is far from compelling.

We applaud Shuker for stating, at last, that the premises of sexual selection are indeed 'refutable' even though he defines sexual selection so as to be at a seemingly safe distance from data that might contradict it. We have received mixed messages from sexual selection advocates in regard to the falsifiability of sexual selection. Shuker, like other participants in this Forum exchange, often writes as though sexual selection is simply inevitable, and that the task of field research is to show how sexual selection is playing out in various species and ecological circumstances. To the contrary, we continue to point out that sexual selection, even in the broad definition that Shuker prefers, is still undemonstrated, and the selective breeding systems theory that derives from sexual selection so as to be at a seemingly safe distance from data that might contradict it. We have received mixed messages from sexual selection advocates in regard to the falsifiability of sexual selection. Shuker, like other participants in this Forum exchange, often writes as though sexual selection is simply inevitable, and that the task of field research is to show how sexual selection is playing out in various species and ecological circumstances. To the contrary, we continue to point out that sexual selection, even in the broad definition that Shuker prefers, is still undemonstrated, and the mating systems theory that derives from sexual selection's definition keeps running afoot of the data.

Finally, we have been asked to comment on the studies of Andersson (1994) and Hoekstra et al. (2001) that summarize positive evidence for sexual selection. Accordingly, we hope it does not seem churlish to criticize work that was state-of-the-art when the truth of sexual selection was not being challenged and the task was to consolidate the available information that seemed to confirm sexual selection. In the present context, however, these summaries are insufficient as evidence that sexual selection exists or is widespread. Andersson reports that his survey of 232 species from studies up to 1990 found 186 species that showed a 'statistical relationship between some character and mating success', including traits such as 'song and display, body size, visual ornaments, and territory or

other resources’ (Andersson & Iwasa 1996, page 56). Andersson also reports that this mating success results from ‘female choice’ for such traits in 167 species and from ‘male contests’ in 58 species. Two difficulties prevent our regarding this summary as conclusive, difficulties acknowledged by Andersson himself, but that seem more significant in the present context than previously.

First, Andersson notes that ‘studies vary in their criteria for mating success; some do not follow success to copulation. Least complete in this respect are the tests that measure female attraction to isolated male traits, for instance loudspeaker tests broadcasting natural or synthetic calls’ (Andersson 1994, page 124). Females can be attracted to males for social reasons other than copulation, such as protection, foraging efficiency and thermoregulation, and therefore some unknown number of studies observed social attraction and not mating success.

Second, Andersson comments that ‘Mating is far from synonymous with fertilization… genetic analysis of paternity is therefore desirable to ensure that mate attraction and copulation are reflected in production of offspring; few studies have yet done so’ (Andersson 1994, page 124). Andersson continues with an important further quotation, ‘even a measure of success based on fertilization is incomplete: what happens to offspring before or at adulthood may depend strongly on rearing conditions and phenotypic or genetic aspects of the parents’. These postmating considerations lie in the area of parental care, a topic Shuker places in mating systems theory, not sexual selection. From our perspective, these offspring-raising considerations are precisely what social selection theory emphasizes: the formation of social groups that act as firms to produce offspring. By our theory, mating per se may be a small, although instrumental, component of the overall reproductive process. Thus, Andersson conceptualizes ‘mating success’ as including what we would consider as part of social selection, namely all activities that lead to increasing the number (rather than the genetic quality) of offspring raised. Hence, evidence Andersson regards as favouring sexual selection might be mixed in with evidence that actually supports social selection.

Hoekstra et al. (2001) provide a quantitative database of selection gradients in the wild that indicate correlations between mating success and various traits. They report that ‘Sexual selection (measured by mating success) appeared stronger than viability selection (measured by survival)’ (page 9157).

As in Andersson’s (1994) compilation, the first difficulty is that the term ‘mating success’ includes a variety of variables such as pairing date, territory tenure or number of pollen per flower. Some of these variables are likely to be more related to other aspects of the breeding system, such as parental care, and thus not be representative of sexual selection (competition for mates) but of social selection (behaviour to maximize number of offspring).

A second difficulty lies in assuming that mating success is the main determinant of fitness. As before, one might find that some trait such as, say, red colour in males is correlated with higher mating success of males. However, the same trait might be negatively correlated with the male’s survival, or with the survival of the offspring into the next generation, resulting in the trait being selectively neutral overall and not serving to indicate genetic quality.

A third difficulty is that the correlation of mating success with the trait may be incidental to the actual selection process. According to social selection the female is behaving to maximize the number of offspring successfully reared. For example, a female might seek safe locations to deposit eggs. Males who can signal such locations will sire offspring because females choose to lay eggs at the locations these males specify. So genes evolve in males to improve signalling clarity, thereby hitchhiking on female choice for safe egg-laying sites. Males with such genes will then appear to enjoy a higher mating success than ineffective signalers, but the females are not choosing males because of those genes: the correlation is incidental to what is actually happening, which is female choice of safe egg-laying sites. This is not sexual selection because the female is not choosing the male, but is choosing egg-laying sites, nor is it competition between males for mates, but simply natural selection for signalling clarity.

Thus, we respect the positive evidence for sexual selection summarized by Andersson (1994) and Hoekstra et al. (2001), among others, but do not find it compelling. As a counterpoint to their positive evidence, we emphasize the growing number of exceptions and discrepancies to sexual selection’s predictions. Citing only positive information on behalf of sexual selection is picking the literature with as much bias as picking only negative information would be. A future research programme should test sexual selection against alternatives, not seek merely to confirm sexual selection.

In ecology, when alternatives to dominant theories have been called for in the past, the prevailing opinion was as confident as today’s is for the generality of sexual selection. In the 1950s density dependence was thought to be inevitable and ubiquitous, in the 1960s the limiting similarity between adjacent niches in niche space was thought to underlie community structure, and in the 1970s benthic species interactions rather than pelagic larval recruitment processes were thought to determine marine population and community dynamics. Today the consensus has shifted on these topics in population and community ecology. We do not know whether the consensus will similarly shift on the inevitability and generality of sexual selection in behavioural ecology, and we will never know unless the need for alternative theories is recognized, and alternatives developed and tested. Therefore, we continue to point out grounds for suspecting that sexual selection will never be substantiated in nature. And we continue to develop and offer alternative framings and formulations for reproductive social behaviour in place of sexual selection and its corollaries and extensions.

We offer no further response to Clutton-Brock (in this issue) and Carranza (in this issue).

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