



Reviews

Sexual selection in females

Tim Clutton-Brock*

Department of Zoology, University of Cambridge

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Darwin developed the theory of sexual selection to account for the evolution of weaponry, ornamentation and other secondary sexual characters that are commonly more developed in males and which appeared unlikely to contribute to survival. He argued that these traits had evolved either through intrasexual competition between males to monopolize access to females or through consistent female preferences for mating with superior partners. Since 1871, a substantial body of research has confirmed his explanation of the evolution of secondary sexual characters in males, although sex differences in reproductive behaviour are more diverse and the evolutionary mechanisms responsible for them are more complex than was initially recognized. However, secondary sexual characters are also widespread in females but, as yet, their evolution and distribution have received relatively little attention from evolutionary biologists. Here, I suggest that the mechanisms responsible for the evolution of secondary sexual characters in females are similar to those operating in males and include intrasexual competition between females for breeding opportunities, male mating preferences and female competition to attract mates. Unlike males, females often compete more intensely for resources necessary for successful reproduction than for access to mating partners and the development of secondary sexual characters in females may be limited by costs to fecundity rather than to survival.

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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

* Correspondence: T. Clutton-Brock, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.
 E-mail address: thcb@cam.ac.uk

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; Ahnesjö 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 I 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 2002; Bjork & Pitnick 2006) 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, *Gobisculus 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, Tettigoniidae, 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 competition with members of other matrilineal lines for rank or access to resources (Hrdy 1981; Walters & Seyfarth 1986; Chapais 1992). For example, in some cercopithecine primates, as well as in some carnivores, females from the same matriline support each other in competitive interactions with members of other matrilineal lines 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 matrilineal lines increases with their size and, in some species, females from dominant matrilineal lines focus their

aggression on female recruits to subordinate matriline (Dittus 1977, 1979; Silk et al. 1981; Clutton-Brock 1991).

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 mates (Herbert 1968; Amundsen 2000a; Kraaijeveld et al. 2007). Male mating preferences have now been documented in insects (Dewsbury 1982; Kvarnemo & Simmons 1999; Bonduriansky 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; Berger 1989; Keddy-Hector 1992; Müller & 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 uninseminated 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; Griggio 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 empidid 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; Erckmann 1981, 1983; Berglund et al. 1986; Oring et al. 1991a; Owens & Thompson 1994; Andersson 1995; Ahnesjö 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; Ahnesjö 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 grillii*, 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 harem groups. 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 and form large mixed-sex herds 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 and adult females show elevated testosterone levels in the later stages of pregnancy (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 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 pseudoscrotum 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 Gossum 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 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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References

- Ahnesjö, I., Kvarnemo, C. & Merilaita, S. 2001. Using potential reproductive rates to predict mating competition among individuals qualified to mate. *Behavioral Ecology*, **12**, 397–401.
- Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M. & Sherman, P. W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans. In: *Evolutionary Biology and Human Social Behavior: an Anthropological Perspective* (Ed. by N. A. Chapman & W. Irons), pp. 402–435. North Scituate, Massachusetts: Duxbury Press.
- Amundsen, T. 2000a. Female ornaments: genetically correlated or sexually selected? In: *Animal Signals: Signalling and Signal Design in Animal Communication* (Ed. by Y. Espmark, T. Amundsen & G. Rosenqvist), pp. 133–154. Trondheim: Tapir Academic Press.
- Amundsen, T. 2000b. Why are female birds ornamented? *Trends in Ecology & Evolution*, **15**, 149–155.
- Amundsen, T. 2000c. Why are female birds ornamented? Reply. *Trends in Ecology & Evolution*, **15**, 471–472.
- Amundsen, T. & Forsgren, E. 2001. Male mate choice selects for female coloration in a fish. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 13155–13160.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Andersson, M. 1995. Evolution of reversed sex roles, sexual size dimorphism and mating system in coucals (Centropodidae, Aves). *Biological Journal of the Linnean Society*, **54**, 173–181.
- Andersson, M. 2004. Social polyandry, parental investment, sexual selection and evolution of reduced female gamete size. *Evolution*, **58**, 24–34.
- Andersson, M. 2005. Evolution of classical polyandry: three steps to female emancipation. *Ethology*, **111**, 1–23.
- Aubin-Horth, N., Desjardins, J. K., Martei, Y. M., Balshine, S. & Hofmann, H. A. 2007. Masculinized dominant females in a cooperatively breeding species. *Molecular Ecology*, **16**, 1349–1358.
- Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity*, **2**, 349–368.
- Bebie, N. & McElligott, A. G. 2006. Female aggression in red deer: does it indicate competition for mates? *Mammalian Biology*, **71**, 347–355.
- Berger, J. 1989. Female reproductive potential and its apparent evaluation by male mammals. *Journal of Mammalogy*, **70**, 347–358.
- Berglund, A. & Rosenqvist, G. 2001. Male pipefish prefer dominant over attractive females. *Behavioral Ecology*, **12**, 402–406.
- Berglund, A. & Rosenqvist, G. 2003. Sex role reversal in pipefish. *Advances in the Study of Behavior*, **32**, 131–167.
- Berglund, A., Rosenqvist, G. & Svensson, I. 1986. Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae). *Behavioral Ecology and Sociobiology*, **19**, 301–307.
- Berglund, A., Rosenqvist, G. & Bernet, P. 1997. Ornamentation predicts reproductive success in female pipefish. *Behavioral Ecology and Sociobiology*, **46**, 145–150.
- Bertram, B. C. R. 1992. *The Ostrich Communal Nesting System*. Princeton, New Jersey: Princeton University Press.
- Bjork, A. & Pitnick, S. 2006. Intensity of sexual selection along the anisogamy-isogamy continuum. *Nature*, **441**, 742–745.
- Blount, J. D., Surai, P. F., Nager, R. G., Houston, D. C., Møller, A. P., Trewby, M. L. & Kennedy, M. W. 2002. Carotenoids and egg quality in the lesser black-backed gull *Larus fuscus*: a supplemental feeding study of maternal effects. *Proceedings of the Royal Society of London, Series B*, **269**, 29–36.
- Bonduriansky, R. 2001. The evolution of male choice in insects: a synthesis of ideas and evidence. *Biological Reviews*, **76**, 305–339.
- Bro-Jørgensen, J. 2007. Reversed sexual conflict in a promiscuous antelope. *Current Biology*, **17**, 2157–2161.
- Burley, N. 1983. The meaning of assortative mating. *Ethology and Sociobiology*, **4**, 191–203.
- Buss, D. M. 1989. Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, **12**, 1–14.
- Carey, J. R. 2001. Demographic mechanisms for the evolution of long life in social insects. *Experimental Gerontology*, **36**, 713–722.
- Chapais, B. 1992. The role of alliances in social inheritance of rank among female primates. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 29–59. Oxford: Oxford University Press.
- Chenoweth, S. F. & Blows, M. W. 2003. Signal trait sexual dimorphism and mutual sexual selection in *Drosophila serrata*. *Evolution*, **57**, 2326–2334.
- Chenoweth, S. F. & Blows, M. W. 2005. Contrasting mutual sexual selection on homologous signal traits in *Drosophila serrata*. *American Naturalist*, **165**, 281–289.
- Chiba, A. & Nakamura, M. 2002. Female cloacal protuberance of the polygynandrous alpine accentor *Prunella collaris*: histological features and possible functional significance. *Ibis*, **144**, E96–E104.

- Chiba, A. & Nakamura, M. 2003. Anatomical and histophysiological characterisation of the male cloacal protuberance of the polygynandrous alpine accentor *Prunella collaris*. *Ibis*, **145**, E83–E93.
- Clark, F. M. & Faulkes, C. G. 1997. Dominance and queen succession in captive colonies of the eusocial mole-rat, *Heterocephalus glaber*. *Proceedings of the Royal Society of London, Series B*, **264**, 993–1000.
- Clutton-Brock, T. H. 1982. The functions of antlers. *Behaviour*, **79**, 108–125.
- Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.
- Clutton-Brock, T. H. 2004. What is sexual selection? In: *Sexual Selection in Primates: New and Comparative Perspectives* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 24–36. Cambridge: Cambridge University Press.
- Clutton-Brock, T. H. 2007. Sexual selection in males and females. *Science*, **318**, 1882–1885.
- Clutton-Brock, T. H. & Harvey, P. H. 1976. Evolutionary rules and primate societies. In: *Growing Points in Ethology* (Ed. by P. P. G. Bateson & R. A. Hinde), pp. 195–237. Cambridge: Cambridge University Press.
- Clutton-Brock, T. H. & Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, **67**, 437–456.
- Clutton-Brock, T. H., Harvey, P. H. & Rudder, B. 1977. Sexual dimorphism, socio-economic sex ratio and body weight in primates. *Nature*, **269**, 797–800.
- Clutton-Brock, T. H., Albon, S. D. & Harvey, P. H. 1980. Antlers, body-size and breeding group size in the Cervidae. *Nature*, **285**, 565–567.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1982. Competition between female relatives in a matrilineal mammal. *Nature*, **300**, 178–180.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, **313**, 131–133.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1988. Reproductive success in male and female red deer. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock), pp. 325–343. Chicago: University of Chicago Press.
- Clutton-Brock, T. H., Brotherton, P. N. M., Smith, R., McIlrath, G., Kansky, R., Gaynor, D., O'Riain, M. J. & Skinner, J. D. 1998. Infanticide and expulsion of females in a cooperative mammal. *Proceedings of the Royal Society of London, Series B*, **265**, 2291–2295.
- Clutton-Brock, T. H., Brotherton, P. N. M., Russell, A. F., O'Riain, M. J., Gaynor, D., Kansky, R., Griffin, A., Manser, M., Sharpe, L., McIlrath, G. M., Small, T., Moss, A. & Monfort, S. 2001. Cooperation, conflict and concession in meerkat groups. *Science*, **291**, 478–481.
- Clutton-Brock, T. H., Hodge, S. J., Spong, G., Russell, A. F., Jordan, N. R., Bennett, N. C. & Manser, M. B. 2006. Intrasexual competition and sexual selection in cooperative meerkats. *Nature*, **444**, 1065–1068.
- Cockburn, A. 2004. Mating systems and sexual conflict. In: *Ecology and Evolution of Cooperative Breeding in Birds* (Ed. by W. Koenig & J. Dickinson), pp. 81–101. Cambridge: Cambridge University Press.
- Craig, I. A. S., Herman, L. M. & Pack, A. A. 2002. Male mate choice and male-male competition co-exist in the humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, **80**, 745–755.
- Creel, S. & Creel, N. M. 2001. *The African Wild Dog: Behavior, Ecology and Conservation*. Princeton, New Jersey: Princeton University Press.
- Crook, J. H. 1972. Sexual selection, dimorphism and social organization in the primates. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 231–281. Chicago: Aldine.
- Cumming, J. M. 1994. Sexual selection and the evolution of dance fly mating systems (Diptera: Empididae; Empidinae). *Canadian Entomologist*, **126**, 907–920.
- Damman, P. & Burda, H. 2005. Sexual activity and reproduction delay ageing in a mammal. *Current Biology*, **16**, 117–118.
- Darwin, C. 1871/1958. *The Descent of Man and Selection in Relation to Sex*. New York: The Modern Library.
- Dewsbury, D. A. 1982. Ejaculate cost and male choice. *American Naturalist*, **119**, 601–610.
- Dewsbury, D. A. 2005. The Darwin–Bateman paradigm in historical context. *Integrative and Comparative Biology*, **45**, 831–837.
- Dittus, W. P. J. 1977. The social regulation of population density and age–sex distribution in the toque monkey. *Behaviour*, **63**, 281–322.
- Dittus, W. P. J. 1979. The evolution of behaviors regulating density and age-specific sex ratios in a primate population. *Behaviour*, **69**, 265–301.
- Dloniak, S. M., French, J. A. & Holekamp, K. E. 2006. Rank-related maternal effects of androgens on behaviour in wild spotted hyenas. *Nature*, **440**, 1190–1193.
- Domb, L. G. & Pagel, M. 2001. Sexual swellings advertise female quality in wild baboons. *Nature*, **410**, 204–206.
- Drea, C. M. 2007. Sex differences and seasonal patterns in steroid secretion in *Lemur catta*: are socially dominant females hormonally masculinized? *Hormones & Behavior*, **51**, 555–567.
- Drea, C. M. & Weil, A. In press. External genital morphology of the ringtailed lemur (*Lemur catta*): females are naturally 'masculinized'. *Journal of Morphology*.
- Drea, C. M., Weldele, M. L., Forger, N., Coscia, E. M., Frank, L. G., Licht, P. & Glickman, S. E. 1998. Androgens and masculinisation of genitalia in the spotted hyena *Crocuta crocuta*: effects of prenatal anti-androgens. *Journal of Reproduction and Fertility*, **113**, 117–127.
- Drea, C. M., Place, N. J., Weldele, M. L., Coscia, E. M., Licht, P. & Glickman, S. E. 2002. Exposure to naturally circulating androgens during fetal life is prerequisite for male mating but incurs direct reproductive costs in female spotted hyenas. *Proceedings of the Royal Society of London, Series B*, **269**, 1981–1987.
- Drickamer, L. C., Gowaty, P. A. & Wagner, D. M. 2003. Free mutual mate preferences in house mice affect reproductive success and offspring performance. *Animal Behavior*, **65**, 105–114.
- East, M. L. & Hofer, H. 2001. Male spotted hyenas (*Crocuta crocuta*) queue for status in social group dominated by females. *Behavioral Ecology*, **12**, 558–568.
- Eens, M. & Pinxten, R. 2000. Sex-role reversal in vertebrates: behavioural and endocrinological accounts. *Behavioural Processes*, **51**, 135–144.
- Ekstrom, J. M. M., Randrianaina, L. & Birkhead, T. R. 2007. Unusual sex roles in a highly promiscuous parrot: the greater vasa parrot *Caracopsis vasa*. *Ibis*, **149**, 313–320.
- Emlen, D. J., Marangelo, J., Ball, B. & Cunningham, C. W. 2005. Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). *Evolution*, **59**, 1060–1084.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- Emlen, S. T. & Wrege, P. H. 2004. Division of labour in parental care behaviour of a sex-role-reversed shorebird, the wattled jacana. *Animal Behaviour*, **68**, 847–855.
- Engh, A. L., Esch, K., Smale, L. & Holekamp, K. E. 2000. Mechanisms of maternal rank inheritance in the spotted hyena, *Crocuta crocuta*. *Animal Behaviour*, **60**, 323–332.
- Erckmann, W. J. 1981. The evolution of sex role reversal and monogamy in shore birds. Ph.D. thesis, University of Washington, Seattle.
- Erckmann, W. J. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. In: *Social Behaviour of Female Vertebrates* (Ed. by S. K. Wasser), pp. 114–168. New York: Academic Press.
- Faulkes, C. G. & Abbott, D. H. 1997. The physiology of a reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. In: *Cooperative Breeding in Mammals* (Ed. by N. G. Solomon & J. A. French), pp. 302–334. Cambridge: Cambridge University Press.
- Fedigan, L. M. 1983. Dominance and reproductive success in primates. *Yearbook of Physical Anthropology*, **26**, 91–129.
- Fisher, D. O., Double, M. C., Blomberg, S. P., Jennions, M. D. & Cockburn, A. 2006. Post-mating sexual selection increases lifetime fitness of polyandrous females in the wild. *Nature*, **444**, 89–91.
- Fivizzani, A. J. & Oring, L. W. 1986. Plasma steroid hormones in relation to behavioural sex role reversal in the spotted sandpiper *Actitis macularia*. *Biology of Reproduction*, **35**, 1195–1201.
- Floody, O. R. 1983. Humans and aggression in female mammals. In: *Hormones and Aggressive Behavior* (Ed. by B. B. Svare), pp. 39–89. New York: Plenum Press.
- Forsgren, E., Amundsen, T., Borg, A. & Bjelvenmark, J. 2004. Unusually dynamic sex roles in a fish. *Nature*, **429**, 551–554.
- Frank, L. G. 1997. Evolution of masculinisation: why do female hyenas have such a large 'penis'? *Trends in Ecology & Evolution*, **12**, 58–62.
- French, J. A. 1997. Proximate regulation of singular breeding in Callitrichid primates. In: *Cooperative Breeding in Mammals* (Ed. by N. G. Solomon & J. A. French), pp. 34–75. Cambridge: Cambridge University Press.
- Ghiselin, M. T. 1974. *The Economy of Nature and the Evolution of Sex*. Berkeley: University of California Press.
- Gilchrist, J. S. 2001. Reproduction and pup care in the communal breeding banded mongoose. Ph.D. thesis, University of Cambridge.
- Glickman, S. E., Coscia, E. M., Frank, L. G., Licht, P., Weldele, M. L. & Drea, C. M. 1998. Androgens and masculinisation of genitalia in the spotted hyena (*Crocuta crocuta*) 3. Effects of juvenile gonads. *Journal of Reproduction and Fertility*, **113**, 129–135.
- Gowaty, P. A. 2004. Sex roles, contests for the control of reproduction and sexual selection. In: *Sexual Selection in Primates* (Ed. by P. Kappeler), pp. 37–54. Cambridge: Cambridge University Press.
- Gowaty, P. A. & Hubbell, S. P. 2005. Chance, time allocation and the evolution of adaptively flexible sex role behavior. *Integrative and Comparative Biology*, **45**, 931–944.
- Gowaty, P. A., Drickamer, L. C. & Schmid-Holmes, S. 2003. Male house mice produce few offspring with lower viability and poorer performance when mated to females they do not prefer. *Animal Behaviour*, **65**, 95–103.
- Goymann, W. & Wingfield, J. C. 2004. Competing females and caring males. Sex steroids in African black coucals, *Centropus grillii*. *Animal Behaviour*, **68**, 733–740.
- Griffin, A. S., Pemberton, J. M., Brotherton, P. N. M., Gaynor, D. & Clutton-Brock, T. H. 2003. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behavioural Ecology*, **14**, 472–480.
- Griggio, M., Valera, F., Casas, A. & Pilastro, A. 2005. Males prefer ornamented females: a field experiment of male choice in the rock sparrow. *Animal Behaviour*, **69**, 1243–1250.
- Harrison, B. J. 1953. Reversal of a secondary sex character by selection. *Heredity*, **7**, 153–164.
- Harvey, P. H., Kavanagh, M. & Clutton-Brock, T. H. 1978. Sexual dimorphism in primate teeth. *Journal of Zoology*, **186**, 475–485.
- Hauber, M. E. & Lacey, E. A. 2005. Bateman's principle in cooperatively breeding vertebrates: the effects of non-breeding alloparents on variability in female and male reproductive success. *Integrative and Comparative Biology*, **45**, 903–914.
- Hawkins, C. E., Dallaas, J. F., Fowler, P. A., Woodroffe, R. & Racey, P. A. 2002. Transient masculinisation in the fossa *Cryptoprocta ferox* (Carnivora, Viverridae). *Biology of Reproduction*, **66**, 610–615.
- Heinsohn, R. G. & Legge, S. 2003. Breeding biology of the reverse-dichromatic, cooperative parrot, *Eclectus oratus*. *Journal of Zoology*, **259**, 197–208.
- Heinsohn, R., Legge, S. & Endler, J. A. 2005. Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science*, **309**, 617–619.

- Herbert, J. 1968. Sexual preference in the rhesus monkey *Macaca mulatta* in the laboratory. *Animal Behaviour*, **16**, 120–128.
- Herdman, E. J. E., Kelly, C. D. & Godin, J.-G. J. 2004. Male mate choice in the guppy (*Poecilia reticulata*): do males prefer larger females as mates? *Ethology*, **110**, 97–111.
- Hodge, S. J., Manica, A., Flower, T. P. & Clutton-Brock, T. H. 2008. Determinants of reproductive success in dominant female meerkats. *Journal of Animal Ecology*, **77**, 92–102.
- Hofer, H. & East, M. L. 2003. Behavioral processes and costs of co-existence in female spotted hyenas: a life-history perspective. *Evolutionary Ecology*, **17**, 315–331.
- Holekamp, K. E. & Smale, L. 2000. Feisty females and meek males: reproductive strategies in the spotted hyena. In: *Reproduction in Context* (Ed. by K. Wallen & J. Schneider), pp. 257–285. Cambridge, Massachusetts: MIT Press.
- Holekamp, K. E., Smale, L. & Szykman, M. 1996. Rank and reproduction in the female spotted hyena. *Journal of Reproduction and Fertility*, **108**, 229–237.
- Houde, A. E. 2001. Sex roles, ornaments, and evolutionary explanation. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 12857–12859.
- Hrdy, S. B. 1981. *The Woman That Never Evolved*. Cambridge, Massachusetts: Harvard University Press.
- Huck, U. W. & Banks, E. M. 1979. Behavioral components of individual recognition in the collared lemming (*Dicrostonyx groenlandicus*). *Behavioral Ecology and Sociobiology*, **6**, 85–90.
- Hunter, J. 1780. Account of an extraordinary pheasant. *Philosophical Transactions of the Royal Society of London*, **70**, 527–535.
- Hunter, J. 1837. An account of an extraordinary pheasant. In: *Observations on Certain Parts of the Animal Oeconomy* (Ed. by R. Owen), pp. 42–48. London: Longman.
- Huxley, J. S. 1938. Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. *American Naturalist*, **72**, 416–433.
- Huxley, J. S. 1942. *Evolution, the Modern Synthesis*. London: Allen & Unwin.
- Isaac, J. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review*, **35**, 101–115.
- Jenni, D. A. 1974. Evolution of polyandry in birds. *American Zoologist*, **14**, 129–146.
- Jones, D. 1996. *Physical Attractiveness and the Theory of Sexual Selection*. Ann Arbor: Museum of Anthropology, University of Michigan.
- Jones, K. M., Monaghan, P. & Nager, R. G. 2001. Male mate choice and female fecundity in zebra finches. *Animal Behaviour*, **62**, 1021–1026.
- Keddy-Hector, A. C. 1992. Mate choice in non-human primates. *American Zoologist*, **32**, 62–70.
- Knickmeyer, R. C. & Baron-Cohen, S. 2006. Foetal testosterone and sex differences in typical social development and in autism. *Journal of Child Neurology*, **21**, 825–845.
- Kraaijeveld, K. 2003. Degree of mutual ornamentation in birds is related to divorce rate. *Proceedings of the Royal Society of London, Series B*, **270**, 1785–1791.
- Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Komdeur, J. 2007. The evolution of mutual ornamentation. *Animal Behaviour*, **74**, 657–677.
- Kuhn, H. J. 1972. On the perineal organ of male *Procolobus badius*. *Journal of Human Evolution*, **1**, 371–378.
- Kvarnemo, C. & Simmons, L. W. 1999. Variance in female quality, operational sex ratio and male mate choice in a bush cricket. *Behavioral Ecology and Sociobiology*, **45**, 245–252.
- Kvarnemo, C., Moore, G. I. & Jones, A. G. 2007. Sexually selected females in the monogamous Western Australian seahorse. *Proceedings of the Royal Society of London, Series B*, **274**, 521–525.
- Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution*, **34**, 292–305.
- Langmore, N. E., Cockren, J. F. & Candy, E. J. 2002. Competition for male reproductive investment elevates testosterone levels in female dunlocks *Prunella modularis*. *Proceedings of the Royal Society of London, Series B*, **269**, 2473–2478.
- LeBas, N. R. 2006. Female finery is not for males. *Trends in Ecology & Evolution*, **21**, 170–173.
- LeBas, N. R. & Marshall, N. J. 2000. The role of colour in signalling and mate choice in the agamid lizard *Ctenophorus ornatus*. *Proceedings of the Royal Society of London, Series B*, **267**, 445–452.
- LeBas, N. R., Hockham, L. R. & Ritchie, M. G. 2003. Nonlinear and correlational sexual selection on 'honest' female ornamentation. *Proceedings of the Royal Society of London, Series B*, **270**, 2159–2165.
- Licht, P., Frank, L. G., Pau, S. C., Yalankaya, T. M., Siiteri, P. K. & Glickman, S. E. 1992. Hormonal correlates of 'masculinization' in female spotted hyena *Crocuta crocuta*. (2) Maternal and fetal steroids. *Journal of Reproduction and Fertility*, **95**, 463–474.
- Licht, P., Hayes, T., Tsai, P., Cunha, G. R., Kim, H., Golbus, M., Hayward, S., Martin, M. C., Jaffe, P. B. & Glickman, S. E. 1998. Androgens and masculinization of genitalia in the spotted hyena *Crocuta crocuta*. (1) Urogenital morphology and placental androgen production during fetal life. *Journal of Reproduction and Fertility*, **113**, 105–115.
- Linville, S. U., Breitwisch, R. & Schilling, A. J. 1998. Plumage brightness as an indicator of parental care in male and female northern cardinals. *Animal Behaviour*, **55**, 119–127.
- Lorch, P. D. 2002. Understanding reversals in the relative strength of sexual selection on males and females: a role for sperm competition? *American Naturalist*, **159**, 645–657.
- McLennan, D. A. 1995. Male mate choice based upon female nuptial coloration in the brook stickleback, *Culaea inconstans* (Kirtland). *Animal Behaviour*, **50**, 213–221.
- Malcolm, J. R. & Marten, K. 1982. Natural selection and the communal rearing of pups in African wild dogs, *Lycaon pictus*. *Behavioral Ecology and Sociobiology*, **10**, 1–13.
- Martin, T. E. & Badyaev, A. V. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. *Evolution*, **50**, 2454–2460.
- Meale, L. 2000. *Sex Differences: Developmental and Evolutionary Strategies*. New York: Academic Press.
- Miller, G., Tybur, J. M. & Jordan, B. D. 2007. Ovulatory cycle effects on tip earnings by lap dancers: economic evidence for human estrus? *Evolution and Human Behavior*, **28**, 375–381.
- Møller, A. P. 1993. Sexual selection in the barn swallow *Hirundo rustica*. III. Female tail ornamentation. *Evolution*, **47**, 417–431.
- Monaghan, P., Metcalfe, N. B. & Houston, D. C. 1996. Male finches selectively pair with fecund females. *Proceedings of the Royal Society of London, Series B*, **263**, 1183–1186.
- Müller, A. E. & Thalmann, U. 2000. Origin and evolution of primate social organisation: a reconstruction. *Biological Reviews*, **75**, 405–435.
- Muller, M. N., Thompson, M. E. & Wrangham, R. W. 2006. Male chimpanzees prefer mating with old females. *Current Biology*, **16**, 2234–2238.
- O'Connor, T., Lee, A., Jarvis, J. U. M. & Buffenstein, R. 2002. Prolonged longevity in naked mole-rats: age-related changes in metabolism, body composition and gastrointestinal function. *Comparative Biochemistry and Physiology*, **133**, 835–842.
- O'Riain, M. J. & Braude, S. 2001. Inbreeding versus outbreeding in captive and wild populations of naked mole-rats. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 143–154. Oxford: Oxford University Press.
- Oring, L. W., Colwell, M. A. & Reed, J. M. 1991a. Lifetime reproductive success in the spotted sandpiper (*Actitis macularia*): sex-differences and variance-components. *Behavioral Ecology and Sociobiology*, **28**, 425–432.
- Oring, L. W., Reed, J. M., Colwell, M. A., Lank, D. B. & Maxson, S. J. 1991b. Factors regulating annual mating success and reproductive success in spotted sandpipers (*Actitis macularia*). *Behavioral Ecology and Sociobiology*, **28**, 433–442.
- Orrell, K. S. & Jensen, T. A. 2002. Male mate choice by the lizard *Anolis carolinensis*: a preference for novel females. *Animal Behaviour*, **63**, 1091–1102.
- Ostner, J., Heislermann, M. & Kappeler, P. M. 2003. Intersexual dominance, masculinized genitals and prenatal steroids: comparative data from primates. *Naturwissenschaften*, **90**, 141–144.
- Owens, I. P. F. & Thompson, D. B. A. 1994. Sex differences, sex ratios and sex roles. *Proceedings of the Royal Society of London, Series B*, **258**, 93–99.
- Packer, C., Collins, D. A., Sindimmo, A. & Goodall, J. 1995. Reproductive constraints on aggressive competition in female baboons. *Nature*, **373**, 60–63.
- Packer, C. R. 1983. Sexual dimorphism: the horns of African antelopes. *Science*, **221**, 1191–1193.
- Palombit, R. A., Cheney, D. L. & Seyfarth, R. M. 2001. Female-female competition for male 'friends' in wild chacma baboons *Papio cynocephalus ursinus*. *Animal Behaviour*, **61**, 1159–1171.
- Parga, J. A. 2006. Male mate choice in *Lemur catta*. *International Journal of Primatology*, **27**, 107–131.
- Pfefferle, D., Heistermann, M., Hodges, J. K. & Fischer, J. 2007. Male Barbary macaques heaviest on mating outcome: a playback study. *Animal Behaviour*, **75**, 1885–1891.
- Pipitone, R. N. & Gallup, G. G. 2008. Women's voice attractiveness varies across the menstrual cycle. *Evolution and Human Behaviour*, **29**, 268–274.
- Plavcan, J. M. 2004. Sexual selection, measures of sexual selection and sexual dimorphism in primates. In: *Sexual Selection in Primates* (Ed. by P. Kappeler & C. van Schaik), pp. 230–252. Cambridge: Cambridge University Press.
- Plusquellec, P. & Boussou, M. F. 2001. Behavioural characteristics of two dairy breeds of cows selected (Hirens) OR not (Bovine des Alpes) for fighting and dominance ability. *Applied Animal Behaviour Science*, **72**, 1–21.
- Preston, B. T., Stevenson, I. R., Pemberton, J. M., Coltman, D. W. & Wilson, K. 2005. Male mate choice influences female promiscuity in Soay sheep. *Proceedings of the Royal Society of London, Series B*, **272**, 365–373.
- Price, T. D. & Birch, G. L. 1996. Repeated evolution of sexual colour dimorphism in passerine birds. *Auk*, **113**, 842–848.
- Racey, P. A. & Skinner, J. D. 1979. Endocrine aspects of sexual mimicry in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology*, **187**, 315–328.
- Reeve, H. K. 1991. Polistes. In: *The Social Biology of Wasps* (Ed. by K. G. Ross & R. W. Mathews), pp. 99–148. New York: Cornell University Press.
- Reeve, H. K. & Ratnieks, F. L. W. 1993. Queen-queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In: *Queen Number and Sociality in Insects* (Ed. by L. Keller), pp. 45–85. Oxford: Oxford University Press.
- Reeve, H. K. & Sherman, P. W. 1991. Intracolony aggression and nepotism by the breeding female naked mole-rat. In: *The Ecology of the Naked Mole-Rat* (Ed. by P. W. Sherman, J. U. M. Jarvis & R. D. Alexander), pp. 337–358. Princeton, New Jersey: Princeton University Press.
- Reinhold, K., Kurtz, J. & Enquist, L. 2002. Cryptic male choice: sperm allocation, strategies when female quality varies. *Journal of Evolutionary Biology*, **15**, 201–209.
- Robertson, A. M. 1985. Female dimorphism and mating behaviour in a damselfly *Ischnura ramburi*: females mimicking males. *Animal Behaviour*, **33**, 805–809.
- Robinson, M. R. & Kruuk, L. E. B. 2007. Function of weaponry in females: the use of horns in intrasexual competition for resources in female Soay sheep. *Biology Letters*, **3**, 651–654.
- Roughgarden, J., Oishi, M. & Akcay, E. 2006. Reproductive social behavior: cooperative games to replace sexual selection. *Science*, **311**, 965–969.
- Ruscio, M. G. & Adkins-Regan, E. 2003. Effect of female brooding behaviour on male mate choice in Japanese quail, *Coturnix japonica*. *Animal Behaviour*, **65**, 397–403.

- Russell, A. F., Carlson, A. A., McIlrath, G. M., Jordan, N. R. & Clutton-Brock, T. H. 2004. Adaptive size modification by dominant female meerkats. *Evolution*, **58**, 1600–1607.
- Sargent, R. C., Gross, M. R. & van den Berghe, E. P. 1986. Male mate choice in fishes. *Animal Behaviour*, **34**, 545–550.
- Schamel, D., Tracy, D. M. & Lank, D. B. 2004. Male mate choice, male availability and egg production as limitations on polyandry in the red-necked phalarope. *Animal Behaviour*, **67**, 847–853.
- Sherman, P. W. & Jarvis, J. U. M. 2002. Extraordinary life spans of naked mole-rats (*Heterocephalus glaber*). *Journal of Zoology*, **258**, 307–311.
- Silk, J. B. 1987. Social behavior in evolutionary perspective. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 318–329. Chicago: University of Chicago Press.
- Silk, J. B. 1997. The function of peaceful post-conflict contacts among primates. *Primates*, **38**, 265–279.
- Silk, J. B., Clark-Wheatley, C. B., Rodman, P. S. & Samuels, A. 1981. Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). *Animal Behaviour*, **29**, 1106–1120.
- Simmons, L. W. 1995. Relative parental investment, potential reproductive roles and the control of sexual selection in katydids. *American Naturalist*, **145**, 797–808.
- Simmons, L. W. & Gwynne, D. T. 1993. Reproductive investment in bush crickets: the allocation of male and female nutrients to offspring. *Proceedings of the Royal Society of London, Series B*, **252**, 1–5.
- Smuts, B. B. 1985. *Sex and Friendship in Baboons*. New York: Aldine.
- Staub, N. L. & de Beer, M. 1997. The role of androgens in female vertebrates. *General and Comparative Endocrinology*, **108**, 1–24.
- Sugiyama, L. S. 2005. Physical attractiveness in adaptationist perspective. In: *The Handbook of Evolutionary Psychology* (Ed. by D. Buss), pp. 292–343. Hoboken, New Jersey: J. Wiley.
- Symons, D. 1979. *The Evolution of Human Sexuality*. Oxford: Oxford University Press.
- Szykman, M., Engh, A. L., van Horn, R. C., Funk, S. M., Scribner, K. T. & Holekamp, K. E. 2001. Association patterns among male and female spotted hyenas (*Crocuta crocuta*) reflect male mate choice. *Behavioral Ecology and Sociobiology*, **50**, 231–238.
- Torres, R. & Velando, A. 2005. Male preference for female foot colour in the socially monogamous blue-footed booby, *Sula nebouxii*. *Animal Behaviour*, **69**, 59–65.
- Trail, P. W. 1990. Why should lek-breeders be monomorphic? *Evolution*, **44**, 1837–1852.
- Tregenza, T. & Wedell, N. 1998. Benefits of multiple males in the cricket *Gryllus bimaculatus*. *Evolution*, **52**, 1726–1730.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine-Atherton.
- Trivers, R. L. 1985. *Social Evolution*. Menlo Park: Benjamin Cummings.
- Van Gossum, H., Stoks, R., Matthysen, F., Valck, F. & de Bruyn, L. 1999. Male choice for female colour morphs in *Ischnura elegans* (Odonata, Coenagrionidae): testing the hypotheses. *Animal Behaviour*, **57**, 1229–1232.
- Van Gossum, H., Stoks, R. & De Bruyn, L. 2001. Male mate choice for female colour morphs: frequency and method dependence. *Animal Behaviour*, **61**, F31–F34.
- Vehrencamp, S. L. 1977. Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris*. *Science*, **197**, 403–405.
- Voigt, C. & Goymann, W. 2007. Sex-role reversal is reflected in the brain of African black coucals (*Centropus grillii*). *Developmental Neurobiology*, **67**, 1560–1573.
- de Waal, F. B. M. 1982. *Chimpanzee Politics*. London: Allen & Unwin.
- Walters, J. R. & Seyfarth, R. M. 1986. Conflict and cooperation. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 306–317. Chicago: University of Chicago Press.
- Weingrill, T. 2000. Infanticide and the value of male–female relationships in mountain chacma baboons. *Behaviour*, **137**, 337–359.
- Werner, N. Y. & Lotem, A. 2003. Choosy males in a haplochromine cichlid: first experimental evidence for male mate choice in a lekking species. *Animal Behaviour*, **66**, 293–298.
- West-Eberhard, M. J. 1979. Sexual selection, social competition and evolution. *Proceedings of the Royal Society of London, Series B*, **123**, 222–234.
- West-Eberhard, M. J. 1983. Sexual selection, social competition and speciation. *Quarterly Review of Biology*, **55**, 155–183.
- West-Eberhard, M. J. 1984. Sexual selection, competitive communication and species-specific signals in insects. In: *Insect Communication* (Ed. by T. Lewis), pp. 283–324. London: Academic Press.
- West-Eberhard, M. J. 1991. Sexual selection and social behavior. In: *Man and Beast Revisited* (Ed. by M. H. Robinson & L. Tiger), pp. 159–172. Washington DC: Smithsonian Institution Press.
- Widemo, M. S. 2006. Male but not female pipefish copy mate choice. *Behavioral Ecology*, **17**, 255–259.
- Wiens, J. J. 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends in Ecology & Evolution*, **16**, 517–523.
- Wilkinson, G. S. 1993. Artificial sexual selection alters allometry in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Genetical Research*, **62**, 213–222.
- Wong, B. B. M. & Jennions, M. D. 2003. Costs influence male mate choice in a freshwater fish. *Biology Letters*, **270**, 36–38.
- Young, A. J. & Clutton-Brock, T. H. 2006. Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters*, **2**, 385–387.
- Zinner, D., Nunn, C., van Schaik, C. P. & Kappeler, P. M. 2004. Sexual selection and exaggerated sexual swellings of female primates. In: *Sexual Selection in Primates* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 71–89. Cambridge: Cambridge University Press.
- Zucker, I. & Wade, G. 1968. Sexual preference of male rats. *Journal of Comparative and Physiological Psychology*, **6**, 816–819.