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Reviews

Sexual selection in females

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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.

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

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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 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 matrilines 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 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