

*Introduction*

# Sexual and social competition: broadening perspectives by defining female roles

Dustin R. Rubenstein\*

*Department of Ecology, Evolution and Environmental Biology, Columbia University,  
10th Floor Schermerhorn Extension, 1200 Amsterdam Avenue, New York, NY 10027, USA*

Males figured more prominently than females in Darwin's view of sexual selection. He considered female choice of secondary importance to male–male competition as a mechanism to explain the evolution of male ornaments and armaments. Fisher later demonstrated the importance of female choice in driving male trait evolution, but his ideas were largely ignored for decades. As sexual selection came to embrace the notions of parent–offspring and sexual conflict, and experimental tests of female choice showed promise, females began to feature more prominently in the framework of sexual selection theory. Recent debate over this theory has centred around the role of females, not only over the question of choice, but also over female–female competition. Whereas some have called for expanding the sexual selection framework to encompass all forms of female–female competition, others have called for subsuming sexual selection within a broader framework of social selection, or replacing it altogether. Still others have argued for linking sexual selection more clearly to other evolutionary theories such as kin selection. Rather than simply debating terminology, we must take a broader view of the general processes that lead to trait evolution in both sexes by clearly defining the roles that females play in the process, and by focusing on intra- and inter-sexual interactions in males and females.

**Keywords:** sexual selection; social selection; kin selection; sexual conflict; female–female competition; female choice

## 1. INTRODUCTION

Darwin was initially puzzled by the elaborate male traits he observed in many species of animals and sought an evolutionary explanation for these secondary sexual characteristics that did not appear to provide any survival advantage [1]. He theorized that these armaments and ornaments (i.e. traits used in competition and mate attraction, respectively) were ultimately used to increase access to mates, particularly by males [2]. Darwin's view of sexual selection took two forms: (i) male–male combat and threat; and (ii) male courtship of females that can influence a female's choice of mates [1,2]. Of course, today we recognize that the opposite also exists, where males choose and females compete, but these are the 'sex role reversal' exception rather than the rule [3]. Darwin emphasized the importance of intra-sexual conflict in males in shaping the evolution of secondary sexual characteristics. While generally in agreement with Darwin's views on natural selection, Wallace was unconvinced by his theory of sexual selection [4]. Central to his scepticism was the role of females in explaining the evolution of secondary sexual characteristics. Wallace did not like the idea of female choice and thought that the presence of elaborate male traits

was an artefact of anatomy and physiology rather than a consequence of sexual competition and choice [5,6]. Moreover, he thought that natural selection acted on female ornaments to become more dull and small, and largely discounted the rarer instances of elaborate female traits [4,7,8]. Darwin himself generally paid less attention to secondary sexual characteristics in females than in males, trying to explain them away as products of selection on males [5].

In recent decades, females have begun to play a more prominent role in empirical and theoretical studies of sexual selection [5]. Fisher [9] was one of the first contemporary biologists to emphasize the role of females and female choice in sexual selection theory, but his ideas about female preferences were not widely accepted until decades later [6]. It was not until theoretical work on parent–offspring [10] and sexual conflict [11] was developed, and experimental tests of female choice became convincing [12], that researchers began to recognize the importance of females in sexual selection theory. More recently, the concept of female–female competition has featured prominently in both empirical and comparative studies of sexual selection and female trait elaboration [13,14], leading to discussions about the breadth of the concept of sexual selection [15–18]. Much of this renewed interest is due to considerations of the social aspects—both in terms of cooperation and conflict—of mating and reproduction in general, which emphasize the causes and consequences

\*dr2497@columbia.edu

One contribution of 11 to a Theme Issue 'Sexual selection, social conflict and the female perspective'.

of social interactions in shaping trait evolution, particularly with respect to females [14–17,19].

Darwin was quite clear that intra-sexual conflict among males was central to the evolution of elaborate male traits [1,2]. We now accept that female choice can often be as important as male–male competition in selecting for male secondary sexual characteristics [3,20,21], and that females in many species have secondary sexual characteristics as elaborate as those of males [5]. In these cases, female–female competition is likely to be important for female trait elaboration [14]. Although some have considered the roles that females play in trait evolution beyond simply female choice [16,17,22,23], how can we best incorporate all types of female interactions into the theory of sexual selection—or should we at all? Whereas some have called for expanding the framework of sexual selection to encompass all forms of female–female competition [15–17], others have called for subsuming it within a broader framework of social selection [24], and still others have called for replacing it with something altogether new [19,25]. A few authors have argued that to fully understand the processes of sexual selection and trait elaboration in both sexes, sexual selection theory needs to link more clearly to other forms of evolutionary theory, such as kin selection [26–30].

The viewpoints of the authors in this themed issue [31] help to shed light on these and other topics by emphasizing the importance of explicitly considering female roles in studies of trait evolution and social competition. In addition to the novel and reinvigorated theoretical models and frameworks presented, a pair of empirical studies examining the brains of fish and the genomes of stalk-eyed flies take a colourful and an integrative look at the evolution of animal traits. Together, this suite of papers presents different perspectives on the role of female–female competition in trait evolution, and new perceptions on how to view and study female choice.

## 2. SOCIAL COMPETITION IN FEMALES

Clutton-Brock [15] was among the first to call for an explicit redefining of sexual selection theory to more broadly encompass female–female competition. In contrast to Darwin, who emphasized male–male competition in sexual selection and trait elaboration [1,2], Clutton-Brock discussed the importance of female–female competition in shaping secondary sexual characters in many species, particularly social ones [15,16]. He was not, however, the first to realize that female–female competition is important for the evolution of elaborate female traits. Crook [32] acknowledged the influence of direct competition among same-sex individuals via social interactions in contexts only indirectly, or even unrelated, to mating as a potential driver of trait evolution. In this issue, Lyon & Montgomerie [24] further argue that sexual selection is a form of what Crook termed ‘social selection’ [32] and involves selection on traits used specifically in mate attraction. According to their view, this broader framework of social selection therefore not only explains the evolution of traits used in

attracting or gaining access to mates (i.e. sexual selection), but also in other signalling contexts unrelated to mating directly, such as the acquisition of social dominance and parent–offspring feeding [24]. West-Eberhard [33,34] was the first to expand upon Crook’s idea of social selection by emphasizing female–female competition in particular. Tobias *et al.* [23] further discuss these ideas here, showing that selection on elaborate female traits often falls outside the limits of traditional sexual selection theory and instead under the wider umbrella of social selection theory.

In the broadest sense, social selection is simply selection resulting from intraspecific social interactions [35,36]. Recent calls to replace sexual selection with a framework of social selection [19,37], however, use a very different definition than the one developed by Crook [32] and extended by West-Eberhard [33,34] and others here [23,24]. According to Roughgarden’s fringe viewpoint (see [38]), which is further extended in this issue [25], social selection is a hypothesis to explain the ‘adaptive function of choosing mates and other actions taken during reproductive social behaviour is to fashion the social infrastructure from which offspring emerge’. Although proposed as an alternative to sexual selection, this view of social selection deals with how social interactions between potential partners or among parents and offspring influence reproductive success. In other words, Roughgarden’s definition focuses on selection of the social context to enhance reproductive success, rather than how selection enhances traits to provide a competitive—and often reproductive—advantage no matter the context. Moreover, selection on secondary sexual characteristics is not explicitly considered in this alternative framework, and therefore it is more akin to mating system theory than to sexual selection theory [39]. Thus, this view of replacing sexual selection theory with social selection theory [25] contrasts sharply with the view that sexual selection should be considered a subset of social selection theory [23,24,32] because they employ different definitions for the same term.

Explicitly incorporating not just social interactions but social behaviour and social evolutionary theory in general into sexual and social selection theory [28–30,40] is also important for understanding the evolution of animal traits. Intraspecific social interactions are most intense in complex societies, where individuals live together in groups [41]. Although cooperation and altruism underlie the social dynamics of most complex animal societies, conflict is an inherent and important part of living in social groups [29,42]. Characteristic of many complex societies is a high degree genetic relatedness among group members [28,40], which is often maintained via kin selection, or reproductive strategies that favour an organism’s relatives [43,44]. Genetic relatedness is not only central to kin selection theory and cooperative altruism [43,44], but also to the degree of conflict that occurs within groups [42,45,46]. Conflict among individuals within groups over breeding opportunities and mating decisions has important consequences for trait evolution, particularly in females [14,29]. Intense female–female competition over reproduction, dominance rank and

other components of social-living are common in many group-living species [47] and may explain some of the extreme female morphological and physiological adaptation in social animals [14,15]. Studying social conflict empirically in complex societies where individuals of both sexes compete for access to breeding opportunities and mates may help us determine whether selection on traits is primarily for access to breeding opportunities (via dominance rank) or access to mates. In other words, examining this competition simultaneously in both males and females might help determine whether traits are likely to be under sexual or social selection, or both. In general, considering the roles of kin selection and other social evolutionary theories in intra- and inter-sexual interactions, as is discussed in this issue by Rubenstein [29] and Pizzari & Gardner [30], may shed new light on studies of animal trait evolution.

### 3. COMPETITION, CHOICE AND THE FUTURE

To fully understand the evolution of animal signals, it is important to recognize that social competition often occurs in both sexes. Male–male competition obviously exists in many species and formed the basis of Darwin's definition of sexual selection [1,2], but female–female competition can also be common and intense, particularly in social animals [15,16]. Although females in many social species have elaborate secondary sexual characteristics [14], the function of these traits is often unknown [29]. It will be important to determine if female traits are used directly to gain access to mates, or if they are used indirectly to gain access to social rank, territories or other types of resources [17,23]. Only once we determine if the same traits function in similar signalling contexts in both sexes, or if different traits are used in the same contexts by different sexes [29], can we really differentiate between the varying perspectives of sexual and social selection theory. Ultimately, taking a broader perspective on sexual and social selection theory, as well as considering the role of social evolutionary theory in this area, may enrich our understanding of the evolution of animal traits.

Despite a need to more broadly consider the role of female–female competition in trait evolution, female choice is still critical to the process and occurs in most species. However, as Prum [4] cautions in this issue, it may be important to initially question, rather than immediately assume, whether female choice for specific traits always occurs. Nonetheless, most researchers tend to agree that female choice is important in most species [3], but what constitutes choice is not always clear because the interests of males and females are often not aligned [48,49]. For example, in species where sexual conflict is intense and males forcibly copulate with mates, as Brennan & Prum [50] argue and Kazancioglu & Alonzo [51] model in this issue, female choice of male advertisement and female resistance to male coercion may not actually be the same phenomenon, even though they are often treated as such [52,53]. Choice itself is a complex process, and modern tools may allow us to dissect the decision-making progress—as well as the

competitive process—at the mechanistic level. As Cummings [54] shows here, employing a behavioural genomics approach to directly study sensory systems in the brain may shed light on the process of mate choice. Such tools may also inform us about sex differences in intrasexual competition, as different hormones and other mechanisms may be related to aggressive interactions in males and females [55,56]. Similarly, as Baker *et al.* [57] demonstrate here, new genomic tools used to study genetic architecture and gene expression will be valuable for not only understanding female choice, but also sexual conflict, sexual dimorphism and other topics related to trait evolution.

In the end, what we call it or how we study it may change over time, but Darwin was—and still is—correct that traits often evolve owing to intra-sexual competition (in both sexes) and can result in inter-sexual choice (also by both sexes). Females are an essential, and often overlooked, component of this process because they often do more than simply choose mates. That is, although we recognize that sexual conflict between males and females is important, females interact not only with males, but also with other females, in both reproductive and non-reproductive contexts. Ultimately, all of these different types of social interactions contribute to the evolution of ornaments and armaments in both sexes. This themed issue [31] emphasizes the importance of explicitly considering a variety of female roles in studies of trait evolution and social competition and reveals a number of novel and integrative avenues for future research in this area. With modern genomic tools and a new desire to critically re-evaluate existing theory and dogma, the future for studies of animal traits looks bright.

I acknowledge the Columbia University Seminar in Population Biology for sponsoring the symposium on *Sexual Selection, Social Conflict and The Female Perspective* that led to this paper and the broader journal issue of the same name. I thank the participants in the symposium and the additional authors of this issue for their willingness to openly discuss past arguments, while also generating new controversies. Carlos Botero, Bruce Lyon, Robert Montgomerie, Richard Prum and Daniel Rubenstein provided thoughtful comment on previous versions of this manuscript. This work was supported by the National Science Foundation (IOS-1121435) and Columbia University.

### REFERENCES

- 1 Darwin, C. 1859 *On the origin of species by natural selection*. London, UK: John Murray.
- 2 Darwin, C. 1871 *The descent of man, and selection in relation to sex*. London, UK: Murray.
- 3 Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
- 4 Prum, R. O. 2012 Aesthetic evolution by mate choice: Darwin's really dangerous idea. *Phil. Trans. R. Soc. B* **367**, 2253–2265. (doi:10.1098/rstb.2011.0285)
- 5 Amundsen, T. 2000 Why are female birds ornamented? *Trends Ecol. Evol.* **15**, 149–155. (doi:10.1016/S0169-5347(99)01800-5)
- 6 Cronin, H. 1991 *The ant and the peacock: altruism and sexual selection from Darwin to today*. Cambridge, UK: Cambridge University Press.

- 7 Wallace, A. R. 1891 *Natural selection and tropical nature*. London, UK: Macmillan.
- 8 Wallace, A. R. 1889 *Darwinism*. London, UK: Macmillan.
- 9 Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford, UK: Clarendon.
- 10 Trivers, R. L. 1974 Parent–offspring conflict. *Am. Zool.* **14**, 249–264.
- 11 Parker, G. A. 1979 Sexual selection and sexual conflict. In *Sexual selection and reproductive conflict in insects* (eds M. S. Blum & N. A. Blum), pp. 123–166. New York, NY: Academic Press.
- 12 Andersson, M. 1982 Female choice selects for extreme tail length in a widowbird. *Nature* **299**, 818–820. (doi:10.1038/299818a0)
- 13 Clutton-Brock, T. H., Hodge, S. J., Spong, G., Russell, A. F., Jordan, N. R., Bennett, N. C., Sharpe, L. L. & Manser, M. B. 2006 Intrasexual competition and sexual selection in cooperative mammals. *Nature* **444**, 1065–1068. (doi:10.1038/nature05386)
- 14 Rubenstein, D. R. & Lovette, I. J. 2009 Reproductive skew and selection on female ornamentation in social species. *Nature* **462**, 786–789. (doi:10.1038/nature08614)
- 15 Clutton-Brock, T. H. 2007 Sexual selection in males and females. *Science* **318**, 1882–1885. (doi:10.1126/science.1133311)
- 16 Clutton-Brock, T. H. 2009 Sexual selection in females. *Anim. Behav.* **77**, 3–11. (doi:10.1016/j.anbehav.2008.08.026)
- 17 Rosvall, K. A. 2011 Intrasexual competition in females: evidence of sexual selection? *Behav. Ecol.* **22**, 1131–1140. (doi:10.1093/beheco/arr106)
- 18 Rosvall, K. A. 2011 By any name, female–female competition yields differential mating success. *Behav. Ecol.* **22**, 1144–1146. (doi:10.1093/beheco/arr111)
- 19 Roughgarden, J., Oishi, M. & Akcay, E. 2006 Reproductive social behavior: cooperative games to replace sexual selection. *Science* **311**, 965–969. (doi:10.1126/science.1110105)
- 20 Kirkpatrick, M. 1987 Sexual selection by female choice in polygynous animals. *Annu. Rev. Ecol. Syst.* **18**, 43–70. (doi:10.1146/annurev.es.18.110187.000355)
- 21 Andersson, M. & Simmons, L. W. 2006 Sexual selection and mate choice. *Trends Ecol. Evol.* **21**, 296–302. (doi:10.1016/j.tree.2006.03.015)
- 22 Stockley, P. & Bro-Jorgensen, J. 2011 Female competition and its evolutionary consequences in mammals. *Biol. Rev.* **86**, 341–366. (doi:10.1111/j.1469-185X.2010.00149.x)
- 23 Tobias, J. A., Montgomerie, R. & Lyon, B. E. 2012 The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Phil. Trans. R. Soc. B* **367**, 2274–2293. (doi:10.1098/rstb.2011.0280)
- 24 Lyon, B. E. & Montgomerie, R. 2012 Sexual selection is a form of social selection. *Phil. Trans. R. Soc. B* **367**, 2266–2273. (doi:10.1098/rstb.2012.0012)
- 25 Roughgarden, J. 2012 The social selection alternative to sexual selection. *Phil. Trans. R. Soc. B* **367**, 2294–2303. (doi:10.1098/rstb.2011.0282)
- 26 Andersson, M. 1984 Evolution of eusociality. *Annu. Rev. Ecol. Syst.* **15**, 165–189.
- 27 Boomsma, J. J. & Ratnieks, F. L. W. 1996 Paternity in eusocial Hymenoptera. *Phil. Trans. R. Soc. Lond. B* **351**, 947–975. (doi:10.1098/rstb.1996.0087)
- 28 Boomsma, J. J. 2007 Kin selection versus sexual selection: why the ends do not meet. *Curr. Biol.* **17**, R673–R683. (doi:10.1016/j.cub.2007.06.033)
- 29 Rubenstein, D. R. 2012 Family feuds: social competition and sexual conflict in complex societies. *Phil. Trans. R. Soc. B* **367**, 2304–2313. (doi:10.1098/rstb.2011.0283)
- 30 Pizzari, T. & Gardner, A. 2012 The sociobiology of sex: inclusive fitness consequences of inter-sexual interactions. *Phil. Trans. R. Soc. B* **367**, 2314–2323. (doi:10.1098/rstb.2011.0281)
- 31 Rubenstein, D. R., Prum, R. O. & Levandowsky, M. (eds) 2012 *Sexual selection, social conflict and the female perspective*. *Phil. Trans. R. Soc. B*.
- 32 Crook, J. H. 1972 Sexual selection, dimorphism and social organization in primates. In *Sexual selection and the descent of man* (ed. B. Campbell), pp. 231–281. Chicago, IL: Aldine.
- 33 West-Eberhard, M. J. 1979 Sexual selection, social competition, and evolution. *Proc. Am. Philos. Soc.* **123**, 222–234.
- 34 West-Eberhard, M. J. 1983 Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155–183. (doi:10.1086/413215)
- 35 Wolf, J. B., Brodie, E. D. & Moore, A. J. 1999 Interacting phenotypes and the evolutionary process. II. Selection resulting from social interactions. *Am. Nat.* **153**, 254–266. (doi:10.1086/303168)
- 36 Nesse, R. M. 2007 Runaway social selection for displays of partner value and altruism. *Biol. Theory* **2**, 143–155. (doi:10.1162/biot.2007.2.2.143)
- 37 Roughgarden, J. & Akcay, E. 2010 Final response: sexual selection needs an alternative. *Anim. Behav.* **79**, e18–e23. (doi:10.1016/j.anbehav.2009.12.029)
- 38 Kavanagh, E. 2006 Letters: debating sexual selection and mating strategies. *Science* **312**, 689–697.
- 39 Shuker, D. M. 2010 Sexual selection: endless forms or tangled bank? *Anim. Behav.* **79**, e11–e17. (doi:10.1016/j.anbehav.2009.10.031)
- 40 Boomsma, J. J. 2009 Lifetime monogamy and the evolution of eusociality. *Phil. Trans. R. Soc. B* **364**, 3191–3207. (doi:10.1098/rstb.2009.0101)
- 41 Alexander, R. D. 1974 The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383. (doi:10.1146/annurev.es.05.110174.001545)
- 42 Ratnieks, F. L. W., Foster, K. R. & Wenseleers, T. 2006 Conflict resolution in insect societies. *Annu. Rev. Entomol.* **51**, 581–608. (doi:10.1146/annurev.ento.51.110104.151003)
- 43 Maynard Smith, J. 1964 Group selection and kin selection. *Nature* **201**, 1145–1147. (doi:10.1038/2011145a0)
- 44 Hamilton, W. D. 1963 Evolution of altruistic behavior. *Am. Nat.* **97**, 354–356. (doi:10.1086/497114)
- 45 Ratnieks, F. L. W. & Reeve, H. K. 1992 Conflict in single-queen Hymenoptera societies: the structure of conflict and processes that reduce conflict in advanced eusocial species. *J. Theor. Biol.* **158**, 33–65. (doi:10.1016/S0022-5193(05)80647-2)
- 46 Keller, L. & Reeve, H. K. 1994 Partitioning of reproduction in animal societies. *Trends Ecol. Evol.* **9**, 98–102. (doi:10.1016/0169-5347(94)90204-6)
- 47 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. *Integr. Comp. Biol.* **45**, 903–914. (doi:10.1093/icb/45.5.903)
- 48 Arnqvist, G. & Rowe, L. 2005 *Sexual conflict*. Princeton, NJ: Princeton University Press.
- 49 Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. 2003 Sexual conflict. *Trends Ecol. Evol.* **18**, 41–47. (doi:10.1016/S0169-5347(02)00004-6)
- 50 Brennan, P. L. R. & Prum, R. O. 2012 The limits of sexual conflict in the narrow sense: new insights from waterfowl biology. *Phil. Trans. R. Soc. B* **367**, 2324–2338. (doi:10.1098/rstb.2011.0284)
- 51 Kazancıoğlu, E. & Alonzo, S. H. 2012 The evolution of optimal female mating rate changes the coevolutionary dynamics

- of female resistance and male persistence. *Phil. Trans. R. Soc. B* **367**, 2339–2347. (doi:10.1098/rstb.2012.0219)
- 52 Gavrillets, S., Arnqvist, G. & Friberg, U. 2001 The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond. B* **268**, 531–539. (doi:10.1098/rspb.2000.1382)
- 53 Rowe, L., Cameron, E. & Day, T. 2005 Escalation, retreat, and female indifference as alternative outcomes of sexually antagonistic coevolution. *Am. Nat.* **165**, S5–S18. (doi:10.1086/429395)
- 54 Cummings, M. E. 2012 Looking for sexual selection in the female brain. *Phil. Trans. R. Soc. B* **367**, 2348–2356. (doi:10.1098/rstb.2012.0105)
- 55 Rubenstein, D. R. & Wikelski, M. 2005 Steroid hormones and aggression in female Galapagos marine iguanas. *Horm. Behav.* **48**, 329–341. (doi:10.1016/j.yhbeh.2005.04.006)
- 56 Voigt, C. C. & Goymann, W. 2007 Sex-role reversal is reflected in the brain of African coucals (*Centropus grillii*). *Dev. Neurobiol.* **67**, 1560–1573. (doi:10.1002/dneu.20528)
- 57 Baker, R. H., Narechania, A., Johns, P. M. & Wilkinson, G. S. 2012 Gene duplication, tissue-specific gene expression and sexual conflict in stalk-eyed flies (Diopsidae). *Phil. Trans. R. Soc. B* **367**, 2357–2375. (doi:10.1098/rstb.2011.0287)