

*Review*

# Sexual selection is a form of social selection

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Social selection influences the evolution of weapons, ornaments and behaviour in both males and females. Thus, social interactions in both sexual and non-sexual contexts can have a powerful influence on the evolution of traits that would otherwise appear to be detrimental to survival. Although clearly outlined by West-Eberhard in the early 1980s, the idea that social selection is a comprehensive framework for the study of ornaments and weapons has largely been ignored. In West-Eberhard's view, sexual selection is a form of social selection—a concept supported by several lines of evidence. Darwin's distinction between natural and sexual selection has been useful, but recent confusion about the limits of sexual selection suggests that some traits are not easily categorized as naturally or sexually selected. Because social selection theory has much to offer the current debates about both sexual selection and reproductive competition in females, it is sometimes viewed, narrowly, to be most useful when considering female roles. However, social selection theory encompasses much more than female reproductive competition. Our goal here was to provide that broader perspective.

**Keywords:** social selection; sexual selection; ornaments; weapons; mate choice; parental choice

## 1. INTRODUCTION

Understanding the traits and mechanisms that mediate social interactions is a major challenge for evolutionary biologists. Social competition occurs in a rich variety of contexts—animals compete over food resources, space, reproduction, mates, social status and even parental care [1–7]. Although competition in these various situations often affects different components of Darwinian fitness, the social interactions themselves are often mediated by similar ornamental signals—weapons and agonistic behaviours—whatever the context. Such traits capture our imagination and attention because they are often beautiful, bizarre and enigmatic. They certainly captured the attention of Charles Darwin [8].

Darwin [8] developed his second evolutionary theory—sexual selection—to explain the evolution of bizarre ornaments and weapons, traits that seemed to pose a particular challenge to his theory of natural selection. Because these traits appeared to be useless in the struggle for survival, Darwin proposed that they could be better explained in the context of social competition for mates, an insight later expanded to include competition for fertilization [9–11]. Darwin [8] was particularly impressed by ornaments and weapons that differed between the sexes [12]—perhaps explaining his focus on competition connected to matings rather than on social competition more broadly defined [13]. After a long period of neglect, interest

in sexual selection was reignited in the 1970s and has remained a focus of intense study ever since. The broad details of sexual selection theory are now well supported by myriad observations and experiments [14] confirming that Darwin's two general processes of sexual selection—mate choice and intrasexual competition over mates—are widespread in nature and that these two mechanisms help explain much about the evolution of weapons and ornamental traits.

For most biologists, the mere presence of gaudy ornaments, weaponry or sexual dimorphism strongly suggests that sexual selection is at play [14]. But consider, for example, a small group of birds with brilliant orange heads, bowing and displaying their highly ornamented plumage to attract the attention of a dull-coloured conspecific watching attentively nearby. This could be a lekking species, like the Andean cock-of-the-rock (*Rupicola peruvianus*), where several bright orange males display, attracting the dull brown females to their lek and, if their courtship is successful, obtaining copulations (figure 1). But this description applies just as well to a completely different type of social interaction, where the competition is not for matings, and the ornamented individuals are babies (figure 1)—in American coot (*Fulica americana*) families, offspring display highly ornamented bright orange feathers to their dull grey parents to obtain food, nourishment that is critical for offspring survival [15]. In coots, adults are choosing among offspring—not mates—but both the ornamental traits that have evolved in the offspring, and the general process that caused their evolution (choice by favouritism), are the same as they would be if those traits were sexually

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Figure 1. Similar ornamental traits are favoured by both mate choice (left, male Andean cock-of-the-rock: photo Pete Morris) and parental choice (right, newly hatched American coot chick: photo Bruce Lyon), showing how similar traits can be favoured by sexual (left) and non-sexual (right) forms of social selection.

selected. Social interactions involving ornamental traits and weapons that occur outside the context of mating and fertilizations suggest that sexual selection is sometimes too narrow a window through which to view the evolution of such traits.

In this paper, we review and evaluate a broadly integrative theory of social trait evolution that connects the diverse social contexts that favour the evolution of ornaments, weapons and competitive social interactions. Three decades ago, Mary Jane West-Eberhard [1–3] outlined a theory of social selection that was distinctly Darwinian in scope, bringing together ideas about the evolution of social behaviour, ornamental traits and weapons into a comprehensive framework, illustrated with examples from sundry corners of the animal kingdom. Social selection theory expands on Darwin's sexual selection insights by demonstrating that social competition in a variety of contexts unrelated to mating will often favour the evolution of the types of ornaments, weapons and behaviours that have incorrectly become narrowly associated with mating alone.

Despite the potential for West-Eberhard's ideas to influence our perspective on social evolution in general, and to clarify recent confusion about sexual selection in particular, her approach is not as widely known as it deserves to be, possibly because the focus of her main paper on the topic [2] was on speciation. It seems that many researchers are either unaware of West-Eberhard's ideas or are under the impression that they apply only narrowly to the study of speciation, the context in which the ideas were presented. Aspects of the general theory have been reviewed several times since West-Eberhard published her ideas, with most reviews tending to focus on subsets of the theory rather than taking an integrative approach to social selection in general. For example, recent reviews have focused on the link between social selection, sexual selection and female (or mutual) ornamentation [16–18]. In a recent book about speciation in birds, Price [19] also provides an excellent overview of forms of social selection involving social competition among adults and discusses the implications

for speciation. He also notes that our intense focus on sexual selection has resulted in the neglect of other forms of social selection. Queller [20] noted the parallels between sexual selection and parental behaviours, both in terms of the choice and competition processes, and in the evolutionary conflicts of interest generated by competing interests. Nesse [21] provided a good overview of the general theory of social selection and focused attention on the social mechanisms that give rise to feedback loops and runaway selection. Rice & Holland [7] reviewed the implications of social competition for genetic conflicts of interest, but the fact that social selection was not discussed suggests that they were unaware of West-Eberhard's ideas [10].

Some of the most widely quoted discussions of social selection have been focused narrowly on the context of female reproductive competition and ornamentation [16,17], suggesting that social selection theory is most useful when looking at female traits. In the present issue, Tobias *et al.* [13] review the implications of social selection theory for the study of female social competition over resources, both reproductive and non-reproductive, and show the utility of social selection theory to understanding the evolution of social traits in females.

In this paper, we focus on social selection theory more generally, looking at the evolution of ornaments and weapons in both sexes to put the study of social selection on females into context. We show how the theory of social selection provides a broad perspective that encompasses and expands upon sexual selection theory. We further show how the social selection approach forces us to focus on the similarities between traits and selective mechanisms influenced by social interactions in a diversity of contexts, not just mating, for both sexes.

## 2. WHAT IS SOCIAL SELECTION?

Sexual selection has long been considered to be a distinct form of natural selection, characterized by what is often perceived to be a unique suite of selective mechanisms and traits [22]. Beginning in the 1960s, however, Wynne-Edwards [23], Crook [5] and Ghiselin [24] all noted that some of the traits that were the special focus of Darwin's theory of sexual selection—ornaments, weapons and display behaviours—also occur in non-sexual contexts, particularly when competitive social interactions are involved. Crook [5] was the first to propose the term 'social selection' to embrace all forms selection driven by social interactions, including sexual selection. He was also one of the first to note the parallels between social dominance for mates and social dominance for other types of limiting resources, such as food and shelter.

West-Eberhard [1,2] discussed these early observations and developed them into a coherent theory. She proposed that social selection is a distinct form of natural selection where the underlying processes that influence selection include any form of intraspecific social competition, both sexual and non-sexual. She focused on intraspecific social competition in its broadest sense and, following Darwin, considered mate choice (and other forms of choice) to be an indirect form of competition whereby potential mates compete to be chosen

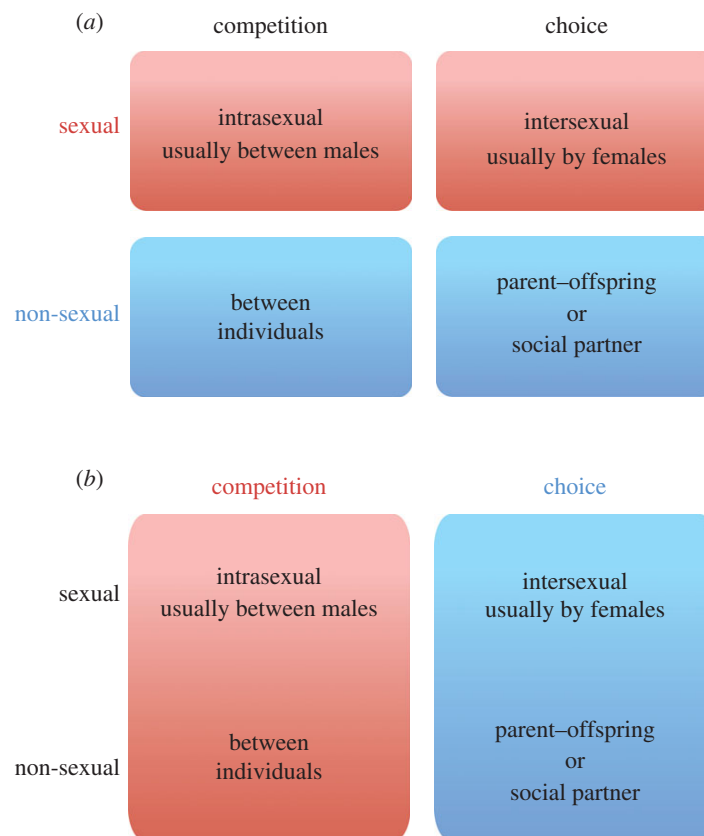


Figure 2. Social selection. (a) As formulated by West-Eberhard [1–3], social selection influences the evolution of ornaments and weapons via choice and competition, respectively, in both sexual and non-sexual contexts. Sexual selection is considered by West-Eberhard to be the subset of social selection where fitness derives from matings and fertilization. (b) Recent empirical research has suggested that there is often no clear boundary between sexual and non-sexual components of social selection while, in contrast, the mechanisms underlying choice and competition may be fundamentally different.

and thus gain access to limiting resources (mates or other resources). In addition to documenting the different non-sexual situations where weapons and ornaments are used by animals, she provided a fundamental insight by noting that Darwin's two mechanisms that shape traits in the sexual arena—competition (intrasexual) and choice (intersexual)—operate during non-sexual interactions as well (figure 2a). In this view (figure 2a), sexual selection is simply the form of social selection that involves fitness advantages relative to mating and fertilization, whereas non-sexual forms of social selection influence other components of fitness such as fecundity or survival. Social selection theory thus helps clarify what is, and what is not, unique about sexual selection—sexual selection is distinctive in terms of fitness consequences (mating/fertilization), but not with respect to the general selective processes (choice or competition) or the resulting traits. Thus, all of the theoretical and methodological approaches that have been so useful for investigating sexual selection can also be applied to the study of social selection. Social selection is generated by competitive social interactions (choice or competition), often leading to the evolution of similar sorts of traits in both sexual and non-sexual contexts.

West-Eberhard [2] presented her ideas about social selection as a narrative, as Darwin did for sexual selection. More recently, quantitative genetic analyses ([6,25–27], among others) have confirmed that trait evolution driven by social interactions has unique properties compared with non-social forms of selection, and

thus that social selection theory describes a coherent, unified evolutionary mechanism [26]. Social selection differs from non-social selection in that an individual's fitness is not solely determined by its own phenotype but also by the phenotypes (and genotypes) of the individuals with which it interacts [26]. The theoretical result is often that indirect genetic effects—where the interacting phenotype is both agent and target of selection—can lead to feedback loops and rapid trait exaggeration [6]. As Wolf *et al.* [26] say about their own model of indirect effects 'Our partitioning of fitness shows that these seemingly disparate factors that generate covariance between a trait providing sexual selection and the traits experiencing social selection can be unified into a single framework. Thus, our model supports West-Eberhard's [1,2] suggestion that there is no fundamental difference between sexual selection, kin selection and other forms of social selection'.

We suggest that three other important attributes further characterize social selection (including sexual selection) compared with non-social selection: (i) fitness typically depends on what others in the population are doing (i.e. a game-theoretical perspective may help us to make sense of the evolution of some traits [28,29]), (ii) social interactions are mediated through signal-receiver systems, with a clear role for sensory systems to shape trait evolution [2,19,30], and (iii) social interactions often lead to intergenomic conflicts of interest and escalated trait evolution in an intraspecific version of the Red Queen mechanism [7]. The obvious





Figure 3. The types of ornaments and weapons produced by sexual selection (top row) are also produced by non-sexual social selection (bottom row). The red epaulettes of red-winged blackbirds (*Agelaius phoeniceus*, top left) are used in territorial defence during the breeding season [32], resulting in enhanced mating success; the colourful crowns of golden-crowned sparrows (*Zonotrichia atricapilla*, bottom left) help win contests over food in winter [33], and winter social dominance correlates with enhanced survival in other bird species. Bird beaks are used as weapons by many birds to defend territories that serve to attract mates, including lark buntings (*Calamospiza melanocorys*, top centre) [34]; beaks are also used as weapons by offspring in species such as laughing kookaburras (*Dacelo novaeguineae*, bottom centre; photo Sarah Legge), wherein siblicide increases food resources for the aggressor, resulting in improved survival [35]. Horns and antlers are favoured by sexual selection in male insects and mammals such as elk (*Cervus canadensis*, top right), where they function as weapons used in fights over females [36]; female beetles (*Onthophagus sagittarius*) use their horns to fight over resources their offspring require [37] (bottom right; photo Sean Stankowski). All photos by Bruce Lyon unless credited otherwise.

congruence between sexual and non-sexual forms of social selection with respect to these characteristics further supports the notion that they together comprise a distinct form of natural selection, as West-Eberhard and others [5] initially proposed. More generally, some attributes of sexual selection that are thought to make it unique with respect to non-sexual forms of natural selection are actually properties shared with social selection.

### 3. COMPETITION AND CHOICE IN A SOCIAL CONTEXT

To illustrate some of these points—and to provide a sense of the scope of social selection theory in general—we present the following five broad examples of social selection in relation to competition and choice, where the parallels to sexual selection are obvious and the general processes are the same (competition and choice), but the traits do not result in increased mating or fertilization success as required by traditional sexual selection theory.

First, the occurrence of intrasexual competition for mates—the major early focus of research on sexual selection [31]—has clear counterparts in non-sexual contexts (figure 3). For example, many male and female birds use ornamental plumage traits as badges of status during dominance interactions in winter flocks (figure 3) [30,38]. Experiments in many species confirm that such badges influence the outcome of interactions over food (and possibly other resources) [30,38] both within and between the sexes. Variation in ornament size typically arises from a post-breeding moult and thus has no immediate reproductive function. It is likely that birds with larger badges survive the winter better, and in better condition, but while their body condition might influence their later mating success, the link between these plumage

ornaments and the bird's fertilization success is indirect at best—enhanced condition could, for example, improve an individual's mating success in the next breeding season. Thus, here is a trait that has some of the earmarks of sexual selection as Darwin saw it, but is not involved directly in mating. This trait falls clearly on the non-sexual side of the social selection ledger (figure 2). In other species, territories or dominance hierarchies span both the breeding and non-breeding seasons [39], so distinguishing the relative influence of sexual and non-sexual social selection on trait evolution will often be difficult [13].

Second, non-sexual interactions often involve the same sort of weaponry influenced by intrasexual selection. For example, sibling rivalry is widespread in nature, and competition for limiting parental resources can often favour the evolution of sibling aggression [40]. Thus, egret chicks use their beaks as weapons to establish dominance hierarchies that influence access to parental food, with strong effects on survival. Such weaponry has been documented in the offspring of a wide variety of taxa where there is intense competition for parental resources [40] (figure 3). This raises the possibility that offspring could also use signals of fighting ability, or badges of status, to settle conflicts over parental resources, but this idea is only just starting to receive attention [41].

Third, in diverse taxa, females compete for resources that affect fecundity, and such competition is often mediated by signals, aggression or weapons [2,42]. Whether or not some of these examples reflect sexual selection is contentious [13], but a broader social selection perspective is useful because it forces us to focus not only on the traits under selection from social competition, but also on the specific fitness component that drives selection for such traits. For example, female beetles use their horns (figure 3) in fights over resources

(brood balls) essential to producing offspring, and this competition selects for a larger horn size [37]. Because the fitness payoff is fecundity rather than matings, the horns provide a clear example of non-sexual social selection. There are similar examples for mammals, where female ungulates use horns to defend resources [43].

Fourth, in some cases, signalling traits influence both social rank and whether or not a female gets to reproduce at all in a given reproductive bout, as in some cooperative societies of insects, birds and mammals [2,44,45]. The study of social rank is both interesting and challenging with respect to the sexual non-sexual continuum [42,44], because the immediate driver of the competition is a social dominance, which then secondarily connects to fitness. Is female fitness in these species ultimately limited only by matings (i.e. sexual selection), by other fitness components such as access to parental care or group resources, by increasing the share of reproductive output (reproductive skew) or by some combination of sexual and non-sexual fitness components? In some cases, the relevant components will be difficult to disentangle because sexual and non-sexual factors are so intertwined [13].

In other cases, however, the answer is straightforward. In many social insect colonies, females compete over skew in reproduction [2], and in some cases, badges of status may mediate the competition [46], although this is somewhat controversial [47]. Because matings occur prior to colony establishment, and these colonies are composed entirely of females, it is a stretch to categorize this female–female competition as sexually selected. A full understanding of social evolution requires that we distinguish among the fitness components that drive the evolution of socially mediated traits.

Fifth, as West-Eberhard [2] pointed out, parental choice is analogous to mate choice except that it operates in a non-sexual context (figure 2). Offspring often depend on their parents for resources—food and shelter—that enhance offspring growth and survival. Thus, when parents control the allocation of these resources, and allocate non-randomly with respect to offspring signalling traits, exaggerated ornaments can evolve in offspring, just as mate choice favours the evolution of such traits in the context of sexual selection. The ornamental plumage of baby American coots (figure 1) described earlier is an obvious example of such a trait that has no relation to sexual selection. The striking natal coats of some primates have been suggested as other examples of parental choice [48]. Choice mechanisms can also apply to other sorts of interactions [21], including partner choice for cooperation [49], male cooperation during reproduction [50] or worker choice of queens in social insect colonies [2]. A fascinating example of worker choice was shown in the red fire ant *Solenopsis invicta*, wherein workers with a particular genetic marker kill queens that lack the marker, possibly using odour cues to identify those queens [51]. This clear example of a ‘green-beard’ recognition mechanism highlights the links between social selection and genetic conflicts of interest [7].

These examples suggest that the sexual and non-sexual aspects of social selection have much in common with respect to the processes of either competition or choice (figure 2a), and the types of traits

involved. Thus, in a way, it would have made as much sense for Darwin (and everybody since) to distinguish between selection based on choice versus competition (figure 2b) rather than on sexual versus non-sexual selection. It is usually quite clear, for example, whether social signals are involved in competition or choice, but many of the same traits are involved in both sexual and non-sexual signalling contexts, as described earlier. Most importantly, the underlying physiological, psychological, ecological and behavioural mechanisms that influence overt competition are largely the same for all kinds of competitive interactions, but may well be different from those involved in parental, social partner and mate choice. Thus, a general understanding of social trait evolution may be confused by the current approach that lumps together very different processes (e.g. intrasexual selection and mate choice), while considering separately the different manifestations of the same processes (e.g. choice or competition in sexual and non-sexual contexts).

#### 4. EXPANDING OUR HORIZONS

To date, Darwinian sexual selection has been the preferred framework for studying the evolution of ornaments and weapons. It is now clear, however, that sexual selection may be too restrictive a focus for understanding the evolution of such traits in a variety of social contexts. Much in the way that Einstein’s theory of general relativity provided a more general explanation of gravity than did Newton’s law of universal gravitation, West-Eberhard’s [2] conception of social selection provides a more general explanation of ornamental traits and weapons than does Darwin’s theory of sexual selection. Similarly, the social selection approach does not render the old paradigm incorrect but instead shows that sexual selection theory can profitably be extended to a much larger set of social phenomena.

Social selection theory is useful because it encourages a change in perspective. Rather than emphasizing the differences between sexual and non-sexual selection (figure 2a), it stimulates us to consider the broad similarities within the processes of competition and choice (figure 2b). With that perspective, the similarities—and in some cases the homologies—are revealed between socially selected traits and the mechanisms that favour them, mechanisms that have heretofore been treated separately as resulting from either sexual or natural selection. Thus, the similarity between the signals of fighting ability used in sexual and non-sexual contexts may extend to their physiological underpinnings—androgens have been found to play a role in signal function in both sexual and non-sexual contexts [30]. Notably, there is recent evidence that this mechanistic overlap extends to aggression among offspring. Female birds in a wide variety of species put sex hormones in their eggs, and there is evidence that these androgens may play a role in sibling competition and aggression in some species [52,53].

There is also a striking overlap between key aspects of mate choice and parental choice. These processes involve two traits of evolutionary interest—the traits that are favoured by choice, and the evolution of choosiness itself. Several mechanisms can influence the evolution of mate choice [14]. Remarkably, all of these have

counterparts in parental choice—sensory bias, honest signalling of genetic quality, direct benefits or manipulation [2,54]. Even Fisher's runaway sexual selection mechanism [55], driven by a genetic correlation between the trait under mate choice and the choice itself, may have a counterpart in parental choice [2,20]. West-Eberhard [2] proposed that the relatedness between parents and offspring creates the genetic correlation between choice and trait needed for a runaway process, a provocative idea that deserves to be modelled explicitly. Intriguingly, similar sorts of genetic correlations are being reported for both mate choice [14,56] and parental choice contexts [57]. The potential for runaway social selection, in general, has begun to receive some attention [21,58].

The evolution of alternative reproductive behaviours (ARBs) provides a clear example where social selection provides a more comprehensive understanding of a phenomenon than sexual selection. ARBs—discrete patterns of morphological or behavioural variation within the sexes that influence reproduction—occur in both males [59,60] and females [4,14,61,62]. However, the sexes differ fundamentally with respect to the context in which the ARBs occur, for an interesting reason. Males of many species engage in ARBs—often involving striking variation in morphology and behaviour—that arise from the key constraint on male reproductive fitness—matings. Thus, in a rich diversity of taxa, a subset of the males are sneakers or female mimics and those tactics enable them to obtain matings without the need to be socially dominant or defend resources [59,60]. In contrast, some female birds, fish and insects are intraspecific brood parasites, bypassing parental care and resource constraints. By laying their eggs in the nests of other conspecifics, these brood parasites are able to realize higher fecundity than they would otherwise, given their social and ecological context [61]. Much of the literature on ARBs focuses exclusively on mating, males and sexual selection and ignores a fairly extensive literature on female alternative reproductive tactics. This narrow perspective deprives us of a richer and more complete understanding of ARBs. The same theoretical framework for alternative tactics applies to both males and females; the main difference is in the fitness components that drive selection for the alternatives. West-Eberhard [4] suggested two decades ago that social selection should favour the evolution of alternative tactics in non-sexual social interactions, just as mating competition favours alternative mating tactics; this idea is well worth exploring.

We believe that a social selection framework for the study of ornaments and weapons (figure 2b) will be of particular interest to those studying the evolution of signals, although the concept of social selection is virtually absent from this literature ([29,30,63], but see [19]). Thus, signals that may well function in mechanistically similar ways (e.g. some badges of status are used during breeding whereas others are used in the non-breeding seasons, or some ornaments are involved in mate choice and others in parental choice) are the subject of different fields of inquiry (e.g. sexual selection versus parental care). However, the underlying mechanisms of any signal-receiver system should be blind to whether the fitness benefit (or costs) to the receiver is survival, fecundity or fertilization success.

Moreover, signals used in social communication are filtered through sensory systems, so it seems likely that there will be aspects of trait evolution that can be explained entirely by features of those sensory systems [19,64] and that such explanations will apply broadly to all contexts of social selection. Signalling theory thus makes perfect sense in the context of social selection, and the recognition of that is bound to foster better communication between those who study signals *per se* and those who study the sexual and non-sexual forms of social selection.

The similarities between sexual and non-sexual social selection with respect to the processes of competition on the one hand, and choice on the other, are both legion and interesting. Could these similarities have deeper genetic roots, in the form of what Shubin *et al.* [65] call 'deep homologies', similarities based on genetic programmes and genomic structures that are ancient in animal lineages? Shubin *et al.* [65] focused on deep homologies with respect to morphology and physiology, but there is every reason to expect them in behaviour too, especially because behaviour is influenced by both morphology and physiology. The social selection framework helps us to recognize these interesting patterns and provides a focus for studying the underlying mechanisms, both behavioural and genetic.

One such genetic example is now well known, involving evolutionary conflicts of interest driven by the social competition that underlies social selection [7,10]. Sexual conflict and parent–offspring conflict are typically considered to be distinctly different genetic conflicts of interest, but Queller [20] pointed out a class of examples where they are indistinguishable—when conflict involves genomic imprinting. Expression of imprinted genes depends on parent of origin. In mammalian embryos, the insulin growth factor gene that promotes enhanced embryonic growth is expressed when paternally inherited, but not when maternally inherited. In contrast, a second gene whose expression is antagonistic to the insulin growth factor is expressed only when maternally inherited [66]. This bizarre genetic conflict blurs the distinction between sexual conflict and parent–offspring conflict [67], a convergence that is less surprising from the social selection perspective where mate choice and parental choice are analogous mechanisms.

## 5. CONCLUSIONS

Sexual selection has been a remarkably successful evolutionary theory, but it is enriched by West-Eberhard's ideas on social selection. Indeed, one clear benefit from social selection's broader perspective is the realization that there is no need to alter sexual selection theory to accommodate a wider array of contexts of social competition, contrary to recent suggestions [42]. Moreover, although sexual selection can reasonably be viewed as a special form of social selection, it is essential to stress that adopting a social selection framework does not require that we abandon the use of the term sexual selection. Sexual selection has a pre-eminent place in evolutionary biology, so it makes sense to continue using the term to describe selection driven by variance in mating and fertilizations, and to use the term social selection as a general umbrella for all forms of social



competition, regardless of fitness component, including sexual selection. Moreover, the term non-sexual social selection can be used to describe selection for traits that clearly enhance components of fitness other than matings [37].

It will not always be easy to distinguish between sexual and non-sexual forms of social selection [13], but a social selection perspective forces us to be more explicit about different fitness components that drive the evolution of ornaments, weapons and social behaviours. In particular, it forces us to consider fitness components other than mating when studying the evolution of these traits. This is important because in some cases, we may not be considering (and testing) all possible selective mechanisms, resulting in a false sense of understanding [68,69]. Revisiting Darwin's book on sexual selection [8] with the benefits of a social selection perspective is intriguing. Darwin devoted considerable attention to bird plumage patterns, many of which strongly supported sexual selection. But, for species where both males and females are brightly coloured, as in many birds, Darwin engaged in logical contortions to interpret the patterns in a way that was consistent with his ideas about male-driven sexual selection [13]. Ironically, many of those bird taxa are the same ones that West-Eberhard [2] used to motivate both general and specific social selection hypotheses—hypotheses that to this day remain largely unexplored, perhaps a casualty of our blinkered focus on sexual selection [19]. Social selection theory extends—and completes—what Darwin began 150 years ago with his theory of sexual selection by providing a more comprehensive framework for understanding social trait evolution.

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## REFERENCES

- West-Eberhard, M. J. 1979 Sexual selection, social competition, and evolution. *Proc. Am. Phil. Soc.* **123**, 222–234.
- West-Eberhard, M. J. 1983 Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155–183. (doi:10.1086/413215)
- West-Eberhard, M. J. 1984 Sexual selection, competitive communication and species-specific signals in insects. In *Insect communication* (ed. T. Lewis), pp. 283–324. New York, NY: Academic Press.
- West-Eberhard, M. J. 1991 Sexual selection and social behavior. In *Man and beast revisited* (eds M. H. Robinson & L. Tiger), pp. 159–172. Washington, DC: Smithsonian 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. B. G. Campbell), pp. 231–281. Chicago, IL: Aldine.
- Moore, A. J., Brodie, E. D. & Wolf, J. B. 1997 Interacting phenotypes and the evolutionary process. I. Direct and indirect genetic effects of social interactions. *Evolution* **51**, 1352–1362. (doi:10.2307/2411187)
- Rice, W. R. & Holland, B. 1997 The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. *Behav. Ecol. Sociobiol.* **41**, 1–10. (doi:10.1007/s002650050357)
- Darwin, C. 1871 *The descent of man, and selection in relation to sex*, vol. 2. London, UK: John Murray.
- Parker, G. A. 1970 Sperm competition and its evolutionary consequences in insects. *Biol. Rev. Camb. Phil. Soc.* **45**, 525–567. (doi:10.1111/j.1469-185X.1970.tb01176.x)
- Arnqvist, G. & Rowe, L. 2005 *Sexual conflict*. Princeton, NJ: Princeton University Press.
- Kokko, H., Jennions, M. D. & Brooks, R. 2006 Unifying and testing models of sexual selection. *Annu. Rev. Ecol. Evol. Syst.* **37**, 43–66. (doi:10.1146/annurev.ecolsys.37.091305.110259)
- Ryan, M. J. 2011 Replication in field biology: the case of the frog-eating bat. *Science* **334**, 1229–1230. (doi:10.1126/science.1214532)
- 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**, 2274–2292. (doi:10.1098/rstb.2011.0280)
- Andersson, M. 1994 *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Lyon, B. E., Eadie, J. M. & Hamilton, L. D. 1994 Parental choice selects for ornamental plumage in American coot chicks. *Nature* **371**, 240–243. (doi:10.1038/371240a0)
- Amundsen, T. 2000 Why are female birds ornamented. *Trends Ecol. Evol.* **15**, 149–155. (doi:10.1016/S0169-5347(99)01800-5)
- Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Komdeur, J. 2007 The evolution of mutual ornamentation. *Anim. Behav.* **74**, 657–677. (doi:10.1016/j.anbehav.2006.12.027)
- Tobias, J. A., Gamarra-Toledo, V., Garcia-Olaechea, D., Pulgarin, P. C. & Seddon, N. 2011 Year-round resource defence and the evolution of male and female song in subsocial birds: social armaments are mutual ornaments. *J. Evol. Biol.* **24**, 2118–2138. (doi:10.1111/j.1420-9101.2011.02345.x)
- Price, T. 2008 *Speciation in birds*. Greenwood Village, CO: Ben Roberts and Company.
- Queller, D. C. 1994 Male–female conflict and parent–offspring conflict. *Am. Nat.* **144**, S84–S99. (doi:10.1086/285654)
- 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)
- Hosken, D. J. & House, C. M. 2011 Sexual selection. *Curr. Biol.* **21**, R62–R65. (doi:10.1016/j.cub.2010.11.053)
- Wynne-Edwards, V. C. 1962 *Animal dispersion in relation to social behaviour*. Edinburgh, UK: Oliver and Boyd.
- Ghiselin, M. T. 1974 *The economy of nature and the evolution of sex*. Berkeley, CA: University of California Press.
- Tanaka, Y. 1996 Social selection and the evolution of animal signals. *Evolution* **50**, 512–523. (doi:10.2307/2410827)
- 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)
- McGlothlin, J. W., Moore, A. J., Wolf, J. B. & Brodie, E. D. 2010 Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution* **64**, 2558–2574. (doi:10.1111/j.1558-5646.2010.01012.x)
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.
- Bradbury, J. W. & Vehrencamp, S. L. 1998 *Principles of animal communication*. Sunderland, MA: Sinauer.

- 30 Searcy, W. A. & Nowicki, S. 2005 *The evolution of animal communication: reliability and deception in signaling systems*. Princeton, NJ: Princeton University Press.
- 31 Emlen, D. J. 2008 The evolution of animal weapons. *Annu. Rev. Ecol. Evol. Syst.* **39**, 387–413. (doi:10.1146/annurev.ecolsys.39.110707.173502)
- 32 Røskoft, E. & Rohwer, S. 1987 An experimental study of the function of the red epaulettes and the black-body color of male red-winged blackbirds. *Anim. Behav.* **35**, 1070–1077. (doi:10.1016/S0003-3472(87)80164-1)
- 33 Chaine, A. S., Tjornell, K. A., Shizuka, D. & Lyon, B. E. 2011 Sparrows use multiple status signals in winter social flocks. *Anim. Behav.* **81**, 447–453. (doi:10.1016/j.anbehav.2010.11.016)
- 34 Chaine, A. S. & Lyon, B. E. 2008 Intrasexual selection on multiple plumage ornaments in the lark bunting. *Anim. Behav.* **76**, 657–667. (doi:10.1016/j.anbehav.2008.03.014)
- 35 Legge, S. 2000 Siblicide in the cooperatively breeding laughing kookaburra (*Dacelo novaeguineae*). *Behav. Ecol. Sociobiol.* **48**, 293–302. (doi:10.1007/s002650000229)
- 36 Lincoln, G. A. 1992 Biology of antlers. *J. Zool.* **226**, 517–528. (doi:10.1111/j.1469-7998.1992.tb07495.x)
- 37 Watson, N. L. & Simmons, L. W. 2010 Reproductive competition promotes the evolution of female weaponry. *Proc. R. Soc. B* **277**, 2035–2040. (doi:10.1098/rspb.2009.2335)
- 38 Rohwer, S. 1977 Status signaling in Harris sparrows—some experiments in deception. *Behaviour* **61**, 107–129. (doi:10.1163/156853977X00504)
- 39 Murphy, T. G., Hernandez-Mucino, D., Osorio-Beristain, M., Montgomerie, R. & Omland, K. E. 2009 Carotenoid-based status signaling by females in the tropical streak-backed oriole. *Behav. Ecol.* **20**, 1000–1006. (doi:10.1093/beheco/arp089)
- 40 Mock, D. W. & Parker, G. A. 1998 *The evolution of sibling rivalry*. New York, NY: Oxford University Press.
- 41 Roulin, A., Kolliker, M. & Richner, H. 2000 Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proc. R. Soc. Lond. B* **267**, 459–463. (doi:10.1098/rspb.2000.1022)
- 42 Clutton-Brock, T. 2009 Sexual selection in females. *Anim. Behav.* **77**, 3–11. (doi:10.1016/j.anbehav.2008.08.026)
- 43 Stankowich, T. & Caro, T. 2009 Evolution of weaponry in female bovids. *Proc. R. Soc. B* **276**, 4329–4334. (doi:10.1098/rspb.2009.1256)
- 44 Clutton-Brock, T. 2007 Sexual selection in males and females. *Science* **318**, 1882–1885. (doi:10.1126/science.1133311)
- 45 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)
- 46 Tibbetts, E. A. & Dale, J. 2004 A socially enforced signal of quality in a paper wasp. *Nature* **432**, 218–222. (doi:10.1038/nature02949)
- 47 Cervo, R., Dapporto, L., Beani, L., Strassmann, J. E. & Turillazzi, S. 2008 On status badges and quality signals in the paper wasp *Polistes dominulus*: body size, facial colour patterns and hierarchical rank. *Proc. R. Soc. B* **275**, 1189–1196. (doi:10.1098/rspb.2007.1779)
- 48 Hrdy, S. B. 1999 *Mother nature*. New York, NY: Pantheon.
- 49 Noe, R. & Hammerstein, P. 1994 Biological markets—supply-and-demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**, 1–11. (doi:10.1007/BF00167053)
- 50 Sinervo, B. & Clobert, J. 2003 Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. *Science* **300**, 1949–1951. (doi:10.1126/science.1083109)
- 51 Keller, L. & Ross, K. G. 1998 Selfish genes: a green beard in the red fire ant. *Nature* **394**, 573–575. (doi:10.1038/29064)
- 52 Schwabl, H. 1993 Yolk is a source of maternal testosterone for developing birds. *Proc. Natl Acad. Sci. USA* **90**, 11 446–11 450. (doi:10.1073/pnas.90.24.11446)
- 53 Schwabl, H., Mock, D. W. & Gieg, J. A. 1997 A hormonal mechanism for parental favouritism. *Nature* **386**, 231. (doi:10.1038/386231a0)
- 54 Kilner, R. M. 2006 Function and evolution of color in young birds. In *Bird coloration*, vol. 2 (eds G. Hill & K. McGraw), pp. 201–232. London, UK: Harvard University Press.
- 55 Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725. (doi:10.1073/pnas.78.6.3721)
- 56 Forstmeier, W., Martin, K., Bolund, E., Schielzeth, H. & Kempenaers, B. 2011 Female extrapair mating behavior can evolve via indirect selection on males. *Proc. Natl Acad. Sci. USA* **108**, 10 608–10 613. (doi:10.1073/pnas.1103195108)
- 57 Kolliker, M., Brinkhof, M. W. G., Heeb, P., Fitze, P. S. & Richner, H. 2000 The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proc. R. Soc. Lond. B* **267**, 2127–2132. (doi:10.1098/rspb.2000.1259)
- 58 Nonacs, P. 2011 Kinship, greenbeards, and runaway social selection in the evolution of social insect cooperation. *Proc. Natl Acad. Sci. USA* **108**, 10 808–10 815. (doi:10.1073/pnas.1100297108)
- 59 Oliveira, R., Taborsky, M. & Brockmann, H. J. 2008 *Alternative reproductive tactics—an integrative approach*. Cambridge, UK: Cambridge University Press.
- 60 Sinervo, B. & Lively, C. M. 1996 The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* **380**, 240–243. (doi:10.1038/380240a0)
- 61 Lyon, B. E. & Eadie, J. M. 2008 Conspecific brood parasitism in birds: a life-history perspective. *Annu. Rev. Ecol. Evol. Syst.* **39**, 343–363. (doi:10.1146/annurev.ecolsys.39.110707.173354)
- 62 Henson, S. A. & Warner, R. R. 1997 Male and female alternative reproductive behaviors in fishes: a new approach using intersexual dynamics. *Annu. Rev. Ecol. Syst.* **28**, 571–592. (doi:10.1146/annurev.ecolsys.28.1.571)
- 63 Zahavi, A. 1991 On the definition of sexual selection, Fisher model, and the evolution of waste and of signals in general. *Anim. Behav.* **42**, 501–503. (doi:10.1016/S0003-3472(05)80052-1)
- 64 Enquist, M. & Arak, A. 1993 Selection of exaggerated male traits by female aesthetic senses. *Nature* **361**, 446–448. (doi:10.1038/361446a0)
- 65 Shubin, N., Tabin, C. & Carroll, S. 2009 Deep homology and the origins of evolutionary novelty. *Nature* **457**, 818–823. (doi:10.1038/nature07891)
- 66 Moore, T. & Haig, D. 1991 Genomic imprinting in mammalian development: a parental tug-of-war. *Trend. Genet.* **7**, 45–49. (doi:10.1016/0168-9525(91)90230-N)
- 67 Trivers, R. L. 1974 Parent–offspring conflict. *Am. Zool.* **14**, 249–264. (doi:10.1093/icb/14.1.249)
- 68 Platt, J. R. 1964 Strong inference—certain systematic methods of scientific thinking may produce much more rapid progress than others. *Science* **146**, 347–353. (doi:10.1126/science.146.3642.347)
- 69 Travis, J. 2006 Is it what we know or who we know? Choice of organism and robustness of inference in ecology and evolutionary biology. *Am. Nat.* **167**, 303–314. (doi:10.1086/501507)