



Forum Articles

Do we need a Sexual Selection 2.0?

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

In this paper we show that Clutton-Brock's extension of the theory to females exacerbates the problems with standard sexual-selection theory, compounding the errors already present when the theory is applied specifically to males. We also show that Carranza's redefinition of sexual selection violates the basic canon of science that once a hypothesis has been falsified, it shall not be redefined to

render it true in light of new data, a process that, if allowed, would render any hypothesis infinitely malleable and thus untestable. Overall, we find that replacing the standard theory of sexual selection with some updated version 2.0 is inadvisable. Instead, we note that our proposal for an altogether new theory to replace sexual selection avoids compounding existing errors, is testable, and is possibly correct.

Below, we consider the two papers separately.

EXTENDING SEXUAL SELECTION TO FEMALES

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

Chapter 2 of *The Genial Gene* (Roughgarden 2009) details three categories of objections to sexual selection theory. The first category consists of the many exceptions to the promiscuous-male and choosy-female templates that Darwin stipulates as 'nearly universal' subject only to 'rare exception,' as summarized in 2004 in *Evolution's*

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Rainbow (Roughgarden 2004). Sexual selection advocates dismiss these exceptions because sexual selection is supposedly true in a great majority of cases. None the less, the variety and quantity of exceptions are now known to be enormous and invite suspicion that sexual selection theory was on the wrong track to begin with.

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

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

Still other self-contradictions lurk throughout sexual selection theory. Recent reviews highlighted logical inconsistencies in the theory that supposedly connects parental investment to the very existence of sexual selection (Queller 1997; Houston & McNamara 2002; Kokko & Jennions 2008). Despite this, Clutton-Brock continues to invoke parental investment theory as the correct theoretical explanation for sex roles in sexual selection (Clutton-Brock 2007, 2009).

Thus, Clutton-Brock's confident assertion that sexual selection is well established for males and therefore ripe for extension to females is unwarranted. None the less, Clutton-Brock's review surveys reproductive behaviour in females and proposes to extend the definition of sexual selection to encompass 'all selection processes operating through intrasexual competition for breeding opportunities in either sex' (Clutton-Brock 2009, page 6). Clutton-Brock argues that even in non-sex-role-reversed species, sexual selection in females mirrors that in males, operating through male

mate choice and intrasexual contests. The only major distinction is that females might compete more for resources than males do, as well as for mates, thus implicitly endorsing the dubious assumption that females invariably have the higher parental investment.

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

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

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

REDEFINING SEXUAL SELECTION

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

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

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

Carranza writes, 'Darwin's wording to define sexual selection as the competition for reproduction is not theoretically consistent nowadays'. So Carranza defines 'sexual selection as "those natural selection forces that operate differently in males and females because of the strategies of the sexes"'. He writes that natural selection becomes sexual selection when 'genes have to face

different selective scenarios depending on sex' and goes on to state that 'under this definition, almost all selection is sexual selection'.

Carranza does sexual selection no favour. In an effort to render it always true by definition, he destroys sexual selection's standing as a scientific hypothesis. Thus, we do not find Carranza's proposal for a Sexual Selection 2.0 to be tenable either. Instead, we retain the original statement of Darwin's theory of sexual selection and find the data available today sufficient to regard it as having been falsified.

COMPETITION, COOPERATION AND SOCIAL SELECTION

Our position is that the greatest scientific progress will now be made by offering alternative hypotheses in place of sexual selection.

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

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

Because our original proposal for a new theory to replace sexual selection (Roughgarden et al. 2006) drew much criticism at the time, and still does, two anonymous referees have requested that we address the criticisms to our theory. In the absence of answers to our critics, the referees suggest that attempts to revise sexual selection into version 2.0 would be preferable to its wholesale replacement, or even that the standard version should be considered OK as it currently stands. Of our proposal for a new theory, one referee notes 'how widely the scientific community disagreed with it' and another referee wonders what could produce a 'shift in the consensus view of sexual selection towards the views of the authors [us]'. Well, we responded to the criticisms when they appeared (Kavanagh 2006; see also our online responses on the *Science* Web site and other venues). For the most part, the criticisms have been emotional and less than useful in contributing to constructive discourse. Today, our most recent overall position, including our response to critics, is summarized in *The Genial Gene* (Roughgarden 2009; cf. book reviews in Belden 2009, Odling-Smee 2009, Pruett-Jones, in press and video-blog interview with Robert Wright on 19 April 2009 at <http://bloggingheads.tv/diavlogs/19126>). We note also that consensus is a 'lagging indicator', describing what people have thought in the past, whereas criticism is a 'leading indicator', describing what people might think in the future. The truth of sexual selection will not be decided by vote or

consensus, but by the facts. And it is the facts that are sinking sexual selection. The enormous and still growing evidence against sexual selection is what motivates our call for a new theory and our efforts to provide one. Yet, sexual selection advocates routinely ignore or misinterpret our findings. As an example, our meta-analysis that casts serious doubt upon the validity of good-genes or compatible-genes benefits in avian extrapair paternity (Akçay & Roughgarden 2007b) is either ignored entirely (Griffith & Immler 2009) or worse, cited as supporting these hypotheses (Gangestad & Thornhill 2008). Thus, our position may be far more consistent with available data than the 'consensus' appreciates.

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

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

CONCLUSION

In conclusion, we appreciate the contributions by Clutton-Brock and Carranza to the debate on the future of sexual selection theory. Few people apprehend how grave the deep, broad difficulties are for

sexual selection, and we interpret the Clutton-Brock and Carranza proposals as implicitly acknowledging this situation. However, we also think that neither Clutton-Brock nor Carranza resolves the problems sexual selection theory is facing because the problems are simply unsolvable. Rather than issue a new version of sexual selection, Sexual Selection 2.0, alternatives to the entire theoretical approach may be preferable. We invite readers to consider the alternative approach we have proposed, social selection.

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