Sexual selection: endless forms or tangled bank?

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Few people apprehend how grave the deep, broad difficulties are for sexual selection

Roughgarden & Akçay 2010

For some biologists sexual selection is in trouble. For the first time since the reinvigoration of sexual selection in the 1970s following the effective rediscovery of mate choice (Bateson 1983; Bradbury & Andersson 1987), the validity of sexual selection as a central component of modern evolutionary theory is being challenged (Roughgarden et al. 2006). That paper, in which Roughgarden and colleagues baldly stated that sexual selection was 'wrong', caught evolutionary biologists on the hop (Kavanagh 2006). Since then renewed versions of the challenge to sexual selection have appeared (e.g. Roughgarden 2007; Roughgarden & Akçay 2010), and, as will be obvious from the companion pieces to this article, resolution is still some way off. In addition, core aspects of the theory of sexual selection, including its definition, have also received renewed attention (Clutton-Brock 2007, 2009; Carranza 2009). Here I consider the current status of sexual selection and attempt to make five points. First, sexual selection is best considered as a useful subset of the overall process of natural selection, with which biologists seek to understand the evolution of traits associated with competition for mates. As such, sexual selection shares the logical framework and coherence of its twin sister,

natural selection. Second, the collection of theory (which I will term 'mating systems theory') used in part to predict patterns of sexual selection is not the same as sexual selection itself; mating systems theory attempts to predict how aspects of a species' biology (from its physiology through to ecology) determine what patterns of competition for mates occurs, and whether or not this differs between the sexes (if 'sexes' even exist). Mating systems theory is therefore conceptually analogous to aspects of population ecology theory that predict how organisms compete for other resources, thereby driving natural selection. Third, the action of sexual selection does not depend on whether or not behavioural interactions between mating partners during reproductive episodes are considered cooperative or selfish. Fourth, whether or not there is sexual selection does not depend on what 'roles' different reproductive classes (mating types or sexes) take during reproductive interactions. Fifth, the claim that there is no evidence for sexual selection is false. To make these points, I will describe a view of sexual selection that I consider a consensus view, and use this to consider what should best not be considered sexual selection. First though, I will consider natural selection and why behavioural and evolutionary ecologists choose to go beyond the evolution of fitness to look at individual traits at all.

Natural Selection and Need for Sexual Selection

Evolution by natural selection is driven by competition, be it competition for resources or competition to avoid death, as

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ultimately something limits population growth (Darwin 1859). Competition among organisms can take a bewildering array of forms, the identification of which forms the basis of much of modern population ecology. The resulting evolutionary adaptations to competition are themselves equally bewildering, but include some rather satisfyingly paradoxical traits such as cooperative behaviour and the sacrificing of individual reproduction (West et al. 2007). In the end though, all these various forms of competition boil down to competition among individuals in a population to leave the most offspring. If individuals vary genetically in their ability to leave offspring in the face of the biotic and abiotic environment they occur in, natural selection has to result in the genetic change to the population that we think of as evolution (Endler 1986). This is the syllogism at the heart of Darwinian evolution: if individuals differ in their ability to leave offspring, and if these differences are partly heritable, then evolution has to occur.

Evolution by natural selection is therefore a population genetic process. If the Darwinian syllogism holds we will see a relationship form between genotype and fitness. As such, it is not necessary to specify how this relationship forms, that is, to make the links between genotype and phenotype, and then phenotype and fitness, explicit (e.g. Brookfield 2009). Put another way, the only trait that matters for evolution is fitness. However, the population genetic perspective leaves untouched many aspects of organism biology we might care about, in particular the nature of phenotypes. Animal behaviour of course is all about these phenotypes, and from Darwin onwards animal behaviour researchers interested in evolution have used conceptual tools to explore phenotypic evolution. One such tool, often used implicitly, is to try to partition how selection has 'acted' on different aspects of the phenotype, including across different stages of an organism's life cycle. This tool is distinctly Darwinian, in the sense that Darwin himself used it when talking about selection for particular traits (Darwin 1859). In some cases, we have given names to these components of the overall natural selection process, when it has proved useful to focus on certain aspects of phenotypes and consider how selection has acted on them. One of the most influential has of course been sexual selection.

What is Sexual Selection?

Sexual selection describes the selection of traits associated with competition for mates. As such we can say that sexual selection arises from competition for mates (Andersson 1994). To avoid confusion, I define 'mate' as a reproductive partner with which one or more zygotes are formed (thereby allowing postcopulatory processes). Despite the work of Roughgarden and colleagues, and indeed the recent commentaries by Carranza (2009) and Clutton-Brock (2009), I consider this to be the standard definition of sexual selection. More formally, sexual selection is the relationship between a trait and its effect on fitness through sexual competition. As such, many traits can be thought of as being both naturally and sexually selected, although from a population genetic viewpoint it is all 'natural selection'. The debate about the distinctions between natural and sexual selection has a long history (e.g. see Endler 1986; Andersson 1994), but a few words might be useful here. One can view evolution by natural selection in its simplest form if fitness itself is the trait under selection. Components of this process can be identified and considered separately though, which becomes extremely useful when we turn our attention (out of desire or necessity) to the evolution of certain phenotypic traits, rather than just fitness. Such a view is given by Endler (1986) in his Figure 1.2. Sexual selection is then a component of natural selection. Unfortunately, evolutionary biologists then tend to lump all other components of natural selection together and call this 'natural

selection' (Endler's 'nonsexual selection', or 'narrow-sense natural selection'), often in the context of viability selection (competition for resources and so on such that an organism lives long enough to engage in competition for mates). For instance, sexual selection is often talked of as being 'balanced' by natural selection, as in some models of exaggerated displays or ornaments (Andersson 1994). It probably would be more precise to say that sexual selection may be balanced by other 'components' of natural selection, but use of the term natural selection also to mean viability selection is now familiar and well entrenched.

Additionally, Endler (1986) pointed out that statistical descriptions of genetic change derived from the breeder's equation partition 'selection' from 'heredity' (i.e. separating selection from genetics). Natural or sexual selection (measured or modelled as selection differentials or gradients) is then no longer synonymous with 'evolution by natural/sexual selection'. Selection can occur but there will not be genetic change unless there is heritable variation for the trait. As above, this partition has proved very useful (it is the basis of quantitative genetics modelling for example), but it is again a conceptual tool, as nature is not an animal breeder. Consider again the trait of interest to be fitness itself. A term denoting the additive genetic variance in fitness among individuals in fact encapsulates both the necessary genetic variation required for a genetic response and also the definition of selection itself (fitness differences among individuals), thereby collapsing the partition between selection and heredity, and giving us Fisher's Fundamental Theorem (Fisher 1930). In this article I will consider sexual selection as a component of an overall natural selection process, and inclusive of both selection and heredity.

Competition for mates can occur in very many forms (Darwin 1871; Andersson 1994), and cooperation between individuals is again not precluded (e.g. DuVal 2007), but it is useful to consider competition over quantity and competition over quality. In terms of quantity of mates, the most basic and familiar form of competition for many of us arises over 'none' versus 'some'. It is well known that in some species some individuals of a given class may fail to obtain a mate because of competition (for instance, male elephant seals and female meerkats: Haley et al. 1994; Clutton-Brock et al. 2006). Alternatively, individuals in a population may for the most part all succeed in finding a reproductive partner, in which case competition may become focused on the quality of that partner. If certain individuals represent a better reproductive resource (there will be a greater number of offspring produced by that partnership), it is clear that competition can arise for access to those individuals as reproductive partners, as it can in any other ecological context. How those partners are obtained may vary, from out and out coercion (Clutton-Brock & Parker 1995) to taking advantage of being a limited resource and choosing only to mate with the most appropriate partner(s) (Bateson 1983). It is for this reason that sexual selection is not precluded in strictly monogamous species (Darwin 1871), and mutual mate choice where both members of reproductive pairs make mate choices is now well established (Kraaijeveld et al. 2007; Clutton-Brock 2009). For sexual selection not to occur in a population, there either has to be no scope for competition (partners as resources are not limiting, and all partners are of equal quality), or the outcome of any competition for mates is totally random with respect to the traits expressed by individuals, such that successful partnerships represent a random sample of pairs of individual phenotypes (and thus genotypes). While we cannot claim that competition for reproductive partners, and thus sexual selection, is ubiquitous (and as Roughgarden & Akçay 2010 note, not all sexual selection processes act in all populations at all times), it has been abundantly clear since Darwin that sexual selection describes something that commonly occurs in nature, with effects that are nontrivial at the phenotypic level. And to make

this point extremely clear, for sexual selection to be 'wrong' and not to occur at all (as suggested by Roughgarden et al. 2006), we have to show that one or both of the premises of the syllogism underlying sexual selection are always untrue in natural populations. As such, either there would never be variation among individuals in their success at obtaining (potentially high-quality) mates, and/or there would never be additive genetic variation among individuals in traits that influence this success. Male guppies have pigmentation that influences their success in mate competition. Male guppies have heritable differences in pigmentation. There is sexual selection in guppies (Brooks & Endler 2001). One could go on, but I hope it is sufficient just to note here that, like its twin sister natural selection, sexual selection happens (Andersson 1994).

Viewing sexual selection as competition for mates is to define sexual selection in broad terms. In their commentary in response to Clutton-Brock (2009), Roughgarden & Akçay (2010) suggest that any such broad definition of sexual selection is 'devoid of any specific meaning'. I find this unconvincing, not least because natural selection, which is of course a description of an overall process that is even broader and subsumes all forms of competition among organisms for future genetic representation, seems to have both a pretty clear meaning and great intellectual utility. Why sexual selection should then be singled out for being overly broad is not clear. If we look for similar examples in ecology, do we find that the concept of density dependence is too broad and therefore meaningless because of the almost innumerable ways in which it can be manifested? Sexual selection, like density dependence, may encompass a lot of processes but the logic at its heart is simple and the premises refutable.

Other definitions of sexual selection have made attempts to make explicit just what it is that is being competed over, including fecundity and resource acquisition that increases fecundity (see Clutton-Brock 2007, 2009). Fecundity (which entails how energy to be invested in reproduction is spread among ova) may be both naturally and sexually selected from a phenotypic point of view. In terms of sexual selection, fecundity may be selected if by being more fecund one attracts an individual who is a better reproductive partner in some way. Such sexual selection may of course in turn increase the competition for mate quality (highly fecund partners). However, fecundity can be fixed in a population and sexual selection still act. In contrast to Clutton-Brock (2007, 2009), I would argue that fecundity by itself, when not associated with competition for mates, is best considered as only being naturally selected (even if it leads to sexual dimorphism). Otherwise sexual selection comes to equate itself with natural selection. Clutton-Brock (2009) considered female–female competition for resources as a possible candidate for a sexual selection process, but going down this route of course means that all foraging behaviours (and indeed all behaviours that mean an individual does not die before managing to become reproductively mature) become associated with differences in fecundity (or sperm load say, if we switch attention to males). At this point, the benefit of a conceptual tool that partitions (and names for convenience) different aspects of the population genetic natural selection process becomes moot, and we might as well revert to just thinking about natural selection, a point made by Clutton-Brock (2009). I do not think we need to go that far though. Viewing sexual selection as competition for mates, while general in the sense of covering a wonderfully diverse range of phenotypes, is actually an excellent focus for researchers: is there competition for mates, and does a given trait influence that competition? If a trait does not, then there are plenty of other drivers of ecological competition (for resources, enemy-free space and so on) that may have left their evolutionary mark on a trait.

Although competition for mates can occur in many different contexts (Andersson 1994), some have received rather little attention from behavioural ecologists (a point also made by Clutton-Brock 2009). That lack of attention is historical and it does not in itself represent a statement of what sexual selection 'is'. For example, sexual selection can occur in isogamous species (e.g. Rogers & Greig 2009) even though the seminal monograph of Andersson (1994) is not full of such examples. In a similar vein, both isogamous and anisogamous gametes can compete for reproductive partners in order to create a zygote. In this case, the quantity of partners for a gamete over which competition arises is (usually) zero or one. Gametes may also vary in quality (for instance in terms of resources provided by the parent) and gametes of the complementary sort may compete for access to each other. The role of sexual competition in gamete evolution is now well established (Birkhead et al. 2009).

Competition for mates has the potential to arise among all classes of organisms in a population, and Darwin (1871) famously pointed out the two forms it would take: intraclass competition and interclass choice, where 'choice' refers to aspects of the phenotype that bias the probability that an individual of one class will become the reproductive partner of an individual of the other class (as such, 'choice' may sometimes seem an unfortunate term). In terms of isogamous species, there may therefore be intramating type competition and intermating type choice. In terms of anisogamous gametes, we can envisage intragamete type competition (among sperms and among ova) and intergamete choice (including passive attraction to gametes of certain phenotypes, or by making fertilization for one class of gamete difficult for the other class). However, it is in anisogamous species at the organismal level, with sperm-producing male tissues and ova-bearing female tissues, that sexual selection has been most thoroughly conceptualized and studied.

How Controversial is this View of Sexual Selection?

The extent to which this view of sexual selection is controversial will be in part measured by the number of readers that have already got bored and stopped reading. My perception is that the above represents the consensus among evolutionary biologists of what sexual selection is (and is at the heart of the view of sexual selection given by Andersson 1994). But clearly controversy is in the air. Of course, researchers can call whatever they like sexual selection, but in doing so a clear conceptual framework is needed. I contend that we already have one, and that the 'conceptual malaise' identified by Roughgarden & Akçay (2010) will come as a big surprise to the vast majority of evolutionary biologists. Using the above framework, I will suggest some things that should not be called sexual selection or confused with sexual selection, highlighting where possible the conceptual consequences of ignoring these suggestions.

What Sexual Selection Should Not Be

Sexual selection should not be a description of the difference in how selection has acted on males and females (as suggested by Carranza 2009). While that phenomenon is currently of great interest, and likely to be pervasive in nature, we already consider it sufficiently under the umbrella of sexually antagonistic selection and sexual conflict (Chapman et al. 2003; Arnqvist & Rowe 2005). A difference in selection on traits in males and females (or the influence of sex on selection, to paraphrase Carranza) is not Darwinian sexual selection, not least because these differences may be unrelated to reproduction (ecological selection on dimorphism for example: Shine 1989), and this means that what Carranza would call sexual selection might influence traits not associated with reproduction. This seems a long way from how sexual selection is currently used. Moreover, the fact that isogamous organisms

with sexual reproduction, but no 'sexes', can experience sexual selection pretty much seals the case. I therefore concur with Roughgarden & Akçay (2010) that the attempt by Carranza to change the definition of sexual selection is less helpful than it might be. Of course, sexual selection as currently understood may well have contributed to traits having different fitness effects in males and females, but turning the logic around is problematic.

Sexual selection is also not just intersexual choice, let alone just female choice. As already explained, intra- and interclass processes co-occur within the framework of sexual selection. It seems of little conceptual relevance to use sexual selection exclusively to refer to one aspect of competition for mates, whether or not a topic such as female choice has been popular and/or controversial (reviewed in Clutton-Brock 2009). Likewise, just because female–female competition for mates has perhaps not received the attention (or been as overt) as male–male competition or female choice does not mean it is not a part of sexual selection (Clutton-Brock 2007, 2009). The same is of course true for male mate choice (e.g. Bonduriansky 2001). Claims by Roughgarden & Akçay (2010) that this makes sexual selection too broad are misplaced (see above). One aspect of interclass choice that might need clarifying though is how 'competition' (as in 'competition for mates') fits in. From the point of the class being chosen (in sexual species, males say), we can easily see that males may compete via displays or some such to be the chosen one (Darwin 1871; Andersson 1994). This competition need not 'look' like competition, as the males could all just stand around showing off their morphology, but they are competing to be chosen (in the way flowering plants may compete to be pollinated). What about the class doing the choosing though (females for example)? As mentioned above (and reviewed in Clutton-Brock 2009), there could be active competition among females to be able to choose the best mating partner. However, the competition need not be overt and some choices might just lead to more offspring or fitter offspring (if we allow indirect genetic benefits) than others. Thus it needs to be kept in mind that these mate preferences evolve via intrasexual selection (while having intersexual selection effects on males). This has not always been clear because the evolution of ornaments and the preferences for them is often (and partly correctly) bundled together as intersexual selection. But the selection on the choosers arises because some female choices mean access to higher quality or more attractive mates than others (Kirkpatrick & Ryan 1991; Maynard Smith 1991). Remember that if all females made the same choice, there would be no variation in preference and sexual selection on female preference would stop. If in the next generation all the males displayed the preferred phenotype, all selection would stop on them as well. Thus intrasexual selection (i.e. intrasexual competition for mates) is part and parcel of mate choice, and therefore I do not believe we have a definition of sexual selection that largely confines sexual selection to males (see Clutton-Brock 2007).

Sexual selection is also not the same as what I will call mating systems theory (Trivers 1972; Emlen & Oring 1977; Davies 1991; Clutton-Brock & Parker 1992; Shuster & Wade 2003). Mating systems theory seeks to address why particular mating (or breeding) systems form, and has included what consequences particular kinds of mating system might have for competition for mates, and thus what forms of sexual selection may occur. Broadly speaking then, mating systems theory takes the biology of an organism (from its physiology, through to its life history and ecology) and tries to predict how and when individuals come together to reproduce, and what opportunities there are for competition for mates. At its fullest extent, it is a theory base of when we expect sexual selection to act, not a theory of sexual selection. For example, all sorts of aspects of mating systems theory could be wrong (and the lack of experimental work is surprising,

but that is a different story) with no effect at all on the logical basis of sexual selection detailed above. Understanding why leks form, why harems form, why resource defence evolves, while impacting our ability to predict forms of sexual selection present in a population, does not impact on whether or not sexual selection is actually happening. For that, we just have to test the validity of our two logical premises: variation in success in competition for mates; a heritable component to that variation. This may seem a facile point, but trying to understand the criticisms of Roughgarden and colleagues leads more to mating systems theory than it does to sexual selection per se.

Ecological analogies with respect to natural selection abound. For instance, we might be completely wrong about how trait-mediated or density-mediated competition impacts fitness in a focal population (i.e. their contribution to natural selection), but we can still test evolution by natural selection in our focal population by examining the relationship between fitness and genotype: failure of one does not demand failure of the other. The phenotypes and the components of selection we try to ascribe as important to those phenotypes are typically what interest us most, but our ability to identify selection correctly is irrelevant to the underlying evolutionary process. (Because of this, one could argue that one perhaps shouldn't bother trying to measure selection 'acting' on individual traits at all: Grafen 1987.) We must remember to separate tests of natural or sexual selection from tests of things we think might influence natural or sexual selection. They are not the same thing. Of course, in reality we want to be able to make predictions about when different forms of competition for mates occur, and in which sex or mating type. But how good we are at that is a test of our understanding of mating systems, not a test of the fundamental process of sexual selection. I reiterate this point because clearly our grasp of mating systems is not as complete as we perhaps thought (a point made very clearly by Clutton-Brock 2007, 2009), but to use that to demolish sexual selection is wrong. Now I am aware that this separation may seem a little convenient, a nice way of hiding sexual selection away from some inconvenient truths about our knowledge of the true roles of operational sex ratio, parental investment and the like. But I hope I have stressed clearly enough, especially through analogy with natural selection, that our difficulty in always correctly predicting when 'something' should happen is not the same as saying that the 'something' therefore never happens.

Perhaps most importantly, sexual selection is not dependent on what have been termed 'sex roles' (who chooses, who competes and so on). This is clear from again considering competition for reproductive partners in organisms without sexes, and is also abundantly clear from the many natural systems where both sexes engage in mate choice (Kraaijeveld et al. 2007). It is true that Darwin (1871) did not belabour this point, and that most of his writing on sexual selection proscribed male and female sex roles in a rather 'traditional' way (most, but not all: see below). It is also true that behavioural ecologists may seem to drop by default into assuming that sexual selection comprises 'male–male competition' and 'female choice'. However, one really does not have to go very far to appreciate that behavioural ecologists have not actually been that stupid (reading Andersson 1994 will suffice). One of the most curious aspects of the challenge to sexual selection put forward by Roughgarden and colleagues has been their contention that the existence of 'sex role-reversed' species are in some way fatal to sexual selection. Rather, such species have long been taken to support our ideas of how mating systems work and evolve, especially when we manipulate 'sex role' by manipulating which sex is the more limiting (e.g. Gwynne & Simmons 1990; Simmons & Bailey 1990; Simmons 1992). The fact that individuals of a given class can sometimes be competitive, and sometimes choosy, all

depending on how different aspects of the environment and species' biology influence competition for mates as a whole, fits mating systems theory rather nicely. The problem is we do not yet have all the answers. This may be simply because aspects of a species' biology and ecology that would allow us to make better predictions are poorly known for all but a few species. In any case though, our ability to understand and predict the causation of sex roles is the purview of mating systems theory; sexual selection does not need males or females to have one sex role or another, it just needs competition for mates.

Sexual selection is not the same thing as sexual conflict. The shift in the way we have viewed reproductive interactions over the last century or so has been well documented (e.g. the well-known change in moral status of the dunnock: Davies 1992; Arnqvist & Rowe 2005). This reinterpretation continues, as it should, to this day. Over the last 15 years or so, driven by empirical observations (most notably in insects), the idea of conflict between males and females over reproductive 'decisions' has become a dominant theme (Arnqvist & Rowe 2005). While it is clear that males and females have to cooperate to some extent in order to mate, especially in internally fertilizing species, both theory and (to a lesser extent) experiment have moved us to view the context in which reproductive behaviour evolves as one primarily driven by sexual conflict rather than sexual cooperation. The key of course is the phrase 'to some extent'. In some insect species, male–female reproductive interactions may be brief, with much of the interaction dominated by a mating struggle as males try to force mating (as in seaweed flies or water striders: Rowe et al. 1994; Shuker & Day 2001). In these species, 'to some extent' is not very much. In many other taxa, on the other hand, such as socially monogamous birds, reproductive interactions include significant investment in parental care by both parents, male and female alike (reviewed in Clutton-Brock 1991). In these cases, 'to some extent' may actually be quite a lot.

That said, behavioural ecologists will probably need to continue to explore the relationship between sexual selection and sexual conflict. For instance, given the current re-emergence of the 'good genes' sexual selection debate (as mentioned by Roughgarden & Akçay, 2010) and some of the important structural weaknesses underlying existing models of intersexual choice (outlined by Arnqvist & Rowe 2005), there is a current enthusiasm for sexual conflict models of the evolution of mate preferences (Holland & Rice 1998; Gavrilets et al. 2001; Cameron et al. 2003). In these models, mate preferences (behaviours that bias the mating success of the opposite sex) are in fact the outcome of attempts to limit (implicitly) costly mating interactions, thus 'choosing' individuals that are able to overcome or subvert those attempts (but this is still sexual selection, only 'chase-away' sexual selection in terms of competition among the 'choosy' sex to limit matings to the minimum necessary: Holland & Rice 1998). These models are attractive and have rightfully received a lot of attention (although not necessarily in terms of experimental tests). However, the fact that a sexual conflict over mating can lead to sexual selection does not mean that sexual conflict is sexual selection (or vice versa). The two are definitely at risk of being conflated by the unwary though.

Sexual Reproduction as a Cooperative Venture

One of the main criticisms voiced by Roughgarden & Akçay, in the current article and others, is that the emphasis on sexual competition and conflict fundamentally misunderstands how evolution has shaped reproductive behaviour in animals. Part of this critique is motivated by the use of certain game-theoretical tools, and in particular the impact of the work of Maynard Smith (1982). Their main contention is that evolutionary game theory has

been developed from only one strand of game theory as originally developed by economists such as Nash (Roughgarden & Akçay, 2010). In particular, they argue that Maynard Smith introduced 'competitive' game theory to biology, but failed to introduce 'cooperative' game theory, which is based on between-actor negotiations (although this interpretation of what constitute different strands of game theory is contested: e.g. Dall et al. 2006). At one level it might not seem a particularly important point, not least because much of the sexual selection theory developed (especially in terms of mate choice) has been avowedly population genetic in nature (Kokko et al. 2006). However, clearly game theory, in the guise of evolutionarily stable strategies (ESSs), has penetrated the psyche of behavioural ecology. Has it done so to the detriment of our understanding of sexual selection? I suggest not for three reasons. First, game-theoretical models in behavioural ecology have actually developed over the years to consider behavioural negotiation (e.g. Houston et al. 2005; Johnstone & Hinde 2006). These models generated useful predictions and did so without creating a crisis in evolutionary ecology. Second, much of the context given for this alternative modelling framework sits firmly in the field of the evolution of parental care, not sexual selection at all. Parental care, or more generally the patterns of parental investment within and among the sexes, has been an important component of mating systems theory, from Trivers (1972) onwards. However, parental investment need have no a priori link to the pattern of sexual selection since a whole array of ecological factors may influence how individuals of a class compete for mates (see above). Third, a rigorous critique of sexual selection that calls for a major redefining of what we mean by sexual selection and how we model it surely needs to be one that is broadly applicable across taxa. As an insect behavioural ecologist, it is not at all clear to me how the inclusion of behavioural negotiations in some form of new sexual selection theory could have anything other than a marginal impact on most reproductive interactions in insects. Of course, one could frame any interaction in terms of a 'negotiation' if one wanted, but it is not clear this would be much more than a semantic gesture in many cases. I could repeatedly punch someone and say it was a negotiation, but members of the local constabulary may consider the interaction less than harmonious. Is it really helpful therefore to reimagine vigorous mating struggles and acts that look like rejection behaviour as 'negotiations' (Rowe et al. 1994)? The same of course is likely to be true for sexual selection in plants, if one wishes to look outside animals.

Perhaps the most important point to remember though, which is in fact implicit in the work of Roughgarden and colleagues, is that behavioural negotiations do not 'remove' conflict from mating interactions, because they could only exist and be relevant if there is conflict present in the first place. Rather, negotiations may provide a strategy to ameliorate the expression of conflict, and 'resolve it' even, such that cooperative outcomes result. These outcomes will only arise though if cooperation, be it reached via real-time negotiation or as part of a genetically programmed behavioural repertoire, has a higher inclusive fitness. Organisms will not negotiate just to be 'nice'. In summary, the behavioural tier introduced by Roughgarden and colleagues may prove useful in certain circumstances, but these models cannot redefine sexual selection.

What did Darwin Think?

One aspect of the sustained critique of sexual selection by Roughgarden and colleagues has been that various societal biases associated with gender have detrimentally influenced how scientists have thought about sexual selection. Moreover, it is argued

that this goes right back to Charles Darwin himself (e.g. Roughgarden 2007). The problem of what Darwin really meant has also cropped up in the recent commentaries by Carranza (2009) and Clutton-Brock (2009). One could easily devote many pages to this, but here are two points perhaps worth briefly considering. First, of course scientific interpretations are not immune from the societies in which they are made (sexual selection provides a nice case study after all: Cronin 1992). What matters though is how enlightening those interpretations remain in the face of new data and new interpretations. The fact we are still all thinking about sexual selection is testament to the lasting value of Darwin's insight, even if we may wish he had left us with a clearer sound-bite of a definition. Second, just what did Darwin think? The answer depends on where you look. In their recent biography, Desmond & Moore (2009) detail how Darwin's thoughts on sexual selection developed over time (especially in terms of its relationship with human evolution), and that development was not straightforward. For instance, in a notebook from 1837 Darwin was able to make notes on female–female competition for males (Desmond & Moore 2009), a long way from the classic view of Darwin and his coy, choosy females 'selecting… males, according to their standard of beauty' (Darwin 1859). And similarly, while *The Descent of Man* (Darwin 1871) is undoubtedly home to much of what we now would consider gender-role stereotyping, he was also able to assert that sexual selection 'depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction', a definition notably devoid of explicit gender roles. However, with thoughts developing nonlinearly over time, coupled with the (very frustrating!) 19th Century practice of making often substantial revisions to books for new editions across many years, trying to ascribe to Darwin a definitive view of sexual selection must ultimately be somewhat unsatisfactory (as indeed it would be for anyone; see Reeves 2007 for a similar discussion of attempts to claim the thought processes of Darwin's equally brilliant contemporary John Stuart Mill). Thus, trying to say whether Darwin got it right or wrong on sexual selection is a bit like trying to claim Darwin for religion or atheism: you pay your money and take your choice (of quotations).

Do We Need a New Sexual Selection?

Do we need sexual selection version 2.0? Given the fall and rise of the popularity of intersexual selection since Darwin (Andersson 1994), the discovery of postcopulatory sexual selection (Parker 1970; Eberhard 1996), the change in our understanding of the role females more typically play in mating systems (Reynolds 1996; Clutton-Brock 2009), and a broader appreciation of sexual conflict (Arnqvist & Rowe 2005), it is clear that we are already well past version 2.0. But do we need a fundamental redefining of sexual selection? I argue not. All of these discoveries change our understanding of when and through what mechanism sexual selection might be said to act on individuals (we know there are more ways for individuals to compete for mates than Darwin did), but they do not change (or demand a change of) the fundamental definition of sexual selection. Studying the behavioural underpinnings of sexual selection has revealed endless forms of reproductive diversity, a diversity we are still only at the beginning of trying to come to terms with. The fact that traits are, in phenotypic terms, both naturally and sexually selected, and that the evolution of traits associated with the mating system feed back into the evolutionary mix, means that disentangling these selection pressures can be a formidable task (indeed one worth avoiding if one is only interested in the population genetic consequences of evolution). However, the conceptual structure we have inherited from Darwin, with a few adjustments here and there, is strong in its simplicity

and an extremely useful organizing tool. We should be wary of giving it away too cheaply.

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