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BOOK SYMPOSIUM

Sex and sensibility: The role of social selection

Roughgarden, Joan: The genial gene: Deconstructing Darwinian selfishness. Berkeley: University of California Press, 2009, ix+261pp, $40.00 HB, $18.95 PB

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In the early twentieth century, Conway Lloyd Morgan warned psychologists against describing the behavior of animals in terms of their mental deliberations. In particular, he suggested that animal psychologists should not call behaviors choices unless they had good evidence that the animals were actually choosing—a dig at Darwinian's theory of sexual selection (Morgan 1909). A century later, Joan Roughgarden also seeks to discredit Darwinian sexual selection. Unlike Morgan, however, she offers in its place a complex vision of what animal minds are capable of accomplishing—a cooperative model of the evolution of social behavior in which *everybody* gets to choose, not just females.

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At the heart of Roughgarden’s book is a two-prong strategy: first, she claims that modern sexual selection theory must be rejected; second, she proposes an alternative framework, social selection, to explain the evolution of sexual diversity in the animal kingdom. In many ways, her dismissal of sexual selection in modern evolutionary psychology resonates with ongoing feminist critiques of evolutionary explanations of sex difference. For example, Roughgarden draws readers’ attentions to how narratives about the origins of cooperative care of offspring typically depend on females as “coy” and prone to monogamy, males as “aggressive” and prone to polygamy, and on the resulting differential parental investment. Where do these sexual stereotypes come from? This is where Charles Darwin and his theory of sexual selection enter Roughgarden’s argument; Darwin’s Victorian sensibilities were inseparable from his theories of evolution, especially his theory of sexual selection on which she claims current theories of social evolution are now based. She hopes that by ridding ourselves of sexual selection, therefore, we can also rid ourselves of these hopelessly outdated sexual stereotypes and start building a new evolutionary account of sociality.

Roughgarden’s claim that she has replaced sexual selection theory with something *new* makes historical ontogenetic sense only if the core of sexual selection theory has remained essentially the same—what Darwin proposed in 1859, is what Richard Dawkins meant in 1976, is what biologists study now—albeit more complicated, with a wide array of additional data and secondary theories to support it. Trivers (1972), with a little help from other mathematically inclined biologists like Hamilton (1963; 1964), developed Darwin’s initial seed into a full-fledged theory only in the 1970s. Roughgarden builds her theory of social selection from tools and assumptions that characterized evolutionary theory before scientific interest in sexual selection picked up in the late 1970s, and this legacy forms the basis for her claim that social selection is theoretically independent from the subsequent development of sexual selection. Let me note that Roughgarden’s vision of the history of sexual selection is neither idiosyncratic nor the result of sloppy research—it reflects the carefully crafted and nearly ubiquitous standard history of sexual selection that has been common since the 1980s (Milam 2010).

Yet this historical framework, I believe, does not hold up to scrutiny. Sexual selection research in the 1950s and 1960s offered a rather different image of sex, mate choice, and biological families than became common only a decade later. In developing her model of social selection, Roughgarden draws on this biological literature, making it impossible to distinguish her theory of social selection from past theories of sexual selection. But if social selection is not an alternative to sexual selection, then what is it? Social selection is part of a much larger project, a fascinating re-envisioning of the evolution of social behavior in animals based on an acceptance of the complexity of animal mind that has become current only in the last decade or so. Based on the treatment Roughgarden’s book has already received at the hands of evolutionary biologists who firmly believe the theory of sexual selection has something to offer, I worry that her attempts to dismiss sexual selection as invalid have obscured the potential implications of her theory of social selection.

To assess Roughgarden’s historical framework, we must first turn our attention to Darwin. For Darwin, sexual selection was not simply about male ornaments

(17–19). Sexual selection was his theory to explain all stable intra-specific differences, including why males and females differed in their appearance and behavior, yes, but also differences between races of a single species (Darwin 1871; Desmond and Moore 2009). Whereas natural selection was based on differential survival, sexual selection stemmed from differential reproduction. Once males and females entered into a reproductive bond, they cooperated to survive in the world by raising their young together and dividing the labor according to their seemingly natural talents (Russett 1989), a characteristic Roughgarden attributes to social selection (241–242). Although Roughgarden is largely unconcerned with sexual selection as an explanation of courtship behavior, in the late nineteenth century, sexual selection's few advocates were entranced more by what preceded copulation than they were by the raising of the offspring that they assumed would inevitably follow.

By the first third of the twentieth century, sexual selection had been largely rejected as a mechanism of evolution in animals (Kellogg 1907). Animals, biologists contended, were not capable of choice-based behaviors, including an esthetic choice of mates. Only humans were capable of truly evaluating the comparative worth of two individuals and consciously selecting one as their reproductive partner. Indeed, the rhetoric of female choice within positive eugenic theories of human evolution remained strong through the 1930s. We can see this cognitive division of animals as reactive and humans as capable of forethought and choice in the behavioral theories of the time. European ethologists like Konrad Lorenz and Nikolaas Tinbergen, for example, were fascinated by the ways in which evolution could produce ritualized stereotyped behavior in animals (Lorenz 1937; Tinbergen 1951). In the U.S.A., behaviorists with a comparative psychology bent researched ways in which animals could be taught to react in predictable ways to a given set of circumstances (Watson 1919; Skinner 1938). Both communities ignored choice-based behaviors. Given this context, it is unsurprising that Julian Huxley (1938) panned female choice in animals and that Ronald Fisher's (1930) theory of runaway sexual selection made little impact in the biological community at large.

By the 1960s, however, primatological and anthropological research began to blur the line between human and animal mind emphasized by Fisher and Huxley earlier in the century (Goodall 1967). Coy females, left at home tending the hearth and the children, and aggressive males, roaming in search of meat and reputation on the savannah, resonated with visions of man the hunter, the tool-maker, the head of the family that characterized contemporaneous studies of social structure in baboons and early hominids (DeVore 1968; Fox 1967; Tiger 1969). As biologists increasingly began to suggest that male and female animals of the same species might be subject to different kinds of evolutionary pressures, second-wave feminism encouraged women to resist male hegemony and strike out on their own (Morgan 1972; Slocum 1975; Tanner 1981).

It was in this context that Trivers (1972) and Wilson (1975) picked up the excitement of rationalist individualistic game theory applied to the selection of animals and people. As Dawkins (1976) subsequently elaborates in *The Selfish Gene* (to which Roughgarden's title alludes), sexual selection seemed to explain why males, who needed to be aggressive to survive the cutthroat reality of the natural world, could differ so dramatically in their nature from females, who needed to choose the right male to succeed in their very different quest to raise lots of babies. Males stayed with females because of sex, he suggested, and females stayed with males because of security. Families worked, when they worked at all, through a system of uneasy mutual bribery, not through a Victorian-inflected system of cooperatively divided labor. Lest you think I am framing Dawkins as a puppet of his social milieu, there were other models of reproductive behavior from which he could have drawn in developing the sexual implications of the *Selfish Gene*, and this is critically important for understanding the biological heritage of Roughgarden's book.

In the 1960s and early 1970s, for example, population geneticists were also interested in the evolution of reproductive behavior. For synthesis architect Theodosius Dobzhansky, the evolutionary success of both *Homo sapiens* and *Drosophila* rested in their genetic diversity. He described both as cosmopolitan species in which genetic diversity rested in a large number of small individual variations, spread over the entire population (Dobzhansky 1955, 1962). It was this ubiquitous variation that allowed both humans and fruit flies to adapt so easily to changes in their environment and ensured their evolutionary success. Following this line of thought, a few of Dobzhansky's many scientific collaborators suggested female mate choice might act as one mechanism to maintain just this type of genetic diversity, a phenomenon they dubbed the "rare male effect" (Petit 1958; Ehrman 1970; see also O'Donald 1980). Claudine Petit and Lee Ehrman argued that if females preferred to mate with rare, exotic, or minority males (they used all of those terms), then the offspring from these couplings would also carry the rare alleles. By preferring to mate with such rare males, females were effectively preventing these rare alleles from being lost to the breeding population, and maintaining the genetic diversity of the species. On the one hand, Petit and Ehrman believed the rare male effect was simply another case of frequency-dependent selection (the most common type being found in predator–prey relations). On the other hand, they described the rare male effect as a kind of sexual selection that could act to counter the effects of natural selection in culling the genetic diversity in a population.

Thus, the vision of humanity and animality that Roughgarden would have us ascribe to social selection resonates strongly with some of these earlier views of sexual selection. Roughgarden (237, 240) argues that families should be seen as cooperative units struggling in a harsh world to raise offspring to adulthood, a vision she notes Lack (1968) promoted in the 1960s, but which was quickly overshadowed by Williams' (1966) attack on group-selection theory. Recall, however, that this cooperative breeding would have been familiar to Darwin himself. Additionally, Roughgarden, Ehrman, and Petit share an interest in the genetic consequences of choice rather than the mechanics of courtship display behavior or sexual difference. Both Ehrman and Petit's model of sexual selection and Roughgarden's theory of social selection posit a synergistic benefit to the long-term survival of the species emerging from the cooperation of males and females for the purpose of reproduction (237, 239). She also suggests that evolutionary biologists ought not to think of behavior as the direct outcome of selection, but instead as the result of a developmental program which itself changes in response to evolutionary pressures—a point that Lehrman (1953) pressed home in his critique of Konrad Lorenz's ethological theories and one quickly adopted by Margaret Bastock (1956) in her study of courtship behavior in *Drosophila* (186).

Equally fascinating is how Roughgarden's model differs from these earlier theories in its implicit description of the cognitive ability of animals. Fisher and Huxley both doubted biologists would ever be able to demonstrate true choice in animals. Dobzhansky, Ehrman, and Petit certainly did not discuss the potential for post-coital conflict or cooperation; they were, after all, working on *Drosophila*—at that time the assumed machines of the animal world. Roughgarden, by way of contrast, argues that many animals are capable of forming a familial bond (by agreeing to enter into a relationship that entails care for offspring) and, after the offspring are produced, further negotiating how to divide the care for those offspring (201–203). She deploys a new set of game theoretic tools to model the evolution of social behavior in this cooperative way—Nash bargaining strategies (140–186). These games allow individual players to exchange of information during iterative rounds of play. They have been used widely in the social sciences, as she notes, but not in biology (143–144, n. 13–14). Biologists in the 1950s and 1960s, it seems likely, rejected these tools because they presupposed a level of cognitive development assumed to be unlikely in most animals. Game theory provided a convenient language with which to describe the apparently rational behavior of individuals incapable of reason (Erickson 2006).

Roughgarden is not alone in re-assessing the cognitive abilities of animals. In the last decade, behavioral biologists have supplied an increasingly complex vision of animal mind. Some biologists have suggested that social learning, or the cultural transmission of learned traditions in animal communities, can be seen in the vocal traditions of whale song or the practice of washing sweet potatoes in a group of Japanese macaques (Rendell and Whitehead 2001, Watanabe 1994). Frans de Waal has even suggested a pre-hominid basis for group morality (see Macedo and Ober 2006). Roughgarden, to my knowledge, is the first mathematically inclined evolutionary theorist to take this reinvigorated view of animal mind and develop new analytical tools to reconstruct the evolution of social behavior in animals.

I return now to the claims with which I began. Roughgarden's theory of social selection is not really an alternative to sexual selection as much as it is a return to a set of possibilities and convictions that dominated biologists' discussions of the evolution of social behavior and female choice before the rise of sociobiology in the 1970s. Yet by framing social selection as an alternative to sexual selection, Roughgarden sells herself short. Discussions surrounding the *Genial Gene* do not have to be only arguments over the validity of sexual selection; they could instead be productive discussions about the evolutionary basis of sociality, based on what we have learned about the evolution of animal minds and culture in the 100 years since Morgan.[1]

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[1] Thanks to Angela Potochink for putting together a fascinating session at ISHPSSB 2009 and additionally to Roberta Millstein and Joan Roughgarden for continuing the conversation we began in Brisbane. Sarah Richardson provided helpful comments on an earlier draft of this essay.

Roberta L. Millstein

In *The Genial Gene*, Joan Roughgarden develops and defends a new type of selection, social selection, and argues that it ought to replace sexual selection. However, Roughgarden's claim raises a bit of a puzzle. Even though Darwin and some contemporary evolutionary biologists differentiate natural selection from sexual selection, most contemporary evolutionary biologists do not. Bonner and May's position is typical:

> A more modern view [than Darwin's] sees sexual selection as simply one of many particular facets of general questions of natural selection…the current definition of Darwinian fitness deals with an individual's total genetic input into the next generation, and thus includes consideration of the mating systems and sex ratios along with simple survival to reproductive age (Bonner and May 1981, xxviii).

In other words, on the "received" view, natural selection is an umbrella term, and sexual selection just describes several ways in which reproductive success can occur (discussed below) under that umbrella. But if this is right, and if *social* selection is also a form of natural selection, as Roughgarden herself implies, then it seems as though a switch to social selection would only require tweaking of natural selection models. Indeed, some of Roughgarden's critics have claimed that social selection is merely a version of existing game theoretic approaches (e.g., Lessells et al. 2006).

However, Roughgarden steadfastly maintains that these critics have missed the point—social selection is something new. I defend Roughgarden's claim that social selection is something new but show that it entails considering the different sorts of causal processes proposed, instead of reproductive success alone. A *causal process approach* illuminates what is at stake in the contemporary debate over social selection and what is revolutionary and interesting about Roughgarden's proposal. A causal process approach also vindicates Darwin's claim that sexual selection and natural selection are different, although I do not fully defend that claim here. However, I will *not* take a stand on which of these causal processes are operating in nature; as Roughgarden herself notes, the empirical studies are still in process.

In what follows, I first discuss how sexual selection can be distinguished from natural selection before turning to the distinction between social selection and sexual selection.

What is sexual selection?

As Mead and Arnold (2004) show in detail, there is no one sexual selection model, but rather many models with conflicting assumptions. For example, in some of the models, females choose males for "good genes," but in some, they do not. Some include sexual conflict between the sexes; some do not. And in some, sexual selection acts only on males, whereas in others, it acts on both males and females. Mead and Arnold (2004) argue that many of the key parameters that would discriminate among these models have not been tested; Roughgarden herself primarily presents and criticizes the adaptationist-oriented "good genes" models of sexual selection.[2] This multiplicity of models makes sexual selection difficult to characterize.

Since this presentation must of necessity be brief, I consider Darwin's account of sexual selection. Not all contemporary biologists would agree with Darwin's account, though some of the aforementioned models discussed by Mead and Arnold (2004) are quite congenial to it (e.g., Lande 1980; Kirkpatrick 1982)–but at least it is the common origin of all the contemporary accounts. Darwin first introduced sexual selection in print in *Origin of Species* (1859), but his more developed view appeared in *Descent of Man* (1871). I thus focus my brief analysis on the *Descent*, noting where I think my reading of Darwin differs from Roughgarden's.

Darwin begins his discussion of sexual selection with secondary sexual characters, which he describes as differences between the sexes that "are not directly connected with the act of reproduction" (1871 vol. I, 253). Darwin acknowledges that the distinction between primary and secondary sexual characters is often not clear-cut. But he does think that there are clear-cut *examples* of secondary sexual characters. According to Darwin, males *tend* (he allows for exceptions) to be larger, stronger, more "pugnacious," equipped with more offensive and defensive weapons, more gaudily colored, and endowed with a greater power of song.

Readers familiar with the contemporary literature on sexual selection might wonder why this list does not include males as being more sexually eager than females, with females being "coy". Indeed, Roughgarden sees this idea as central to sexual selection and traces the idea back to Darwin. However, there are only three references to "coyness" in the *Descent*, most notably where Darwin states:

> The female, on the other hand, with the rarest exception, is less eager than the male… she generally 'requires to be courted;' she is coy, and may often be seen endeavouring for a long time to escape from the male (1871 vol. I, 273).

Thus, while it is true that Darwin thinks that (in general) females are coy and males are eager, it is not his central focus. I think that some contemporary sexual selection proponents have read the *Descent* selectively, overlooking the fact that the secondary sexual characters that Darwin seeks to explain via sexual selection are far broader (see, e.g., Darwin 1981 vol. II, 397–398). So if there is "blame" to be cast for making central the idea that females are coy, I cast it on some readers of Darwin, not Darwin himself as Roughgarden does. Moreover, it is clear that for Darwin, "coyness" and other purported secondary sexual characters are phenomena to be explained by sexual selection, not part of the theory of sexual selection itself. Thus, when some contemporary proponents of sexual selection argue that "choosiness" implies "coyness",[3] they are confusing a phenomenon that Darwin sought to explain (coyness) with part of the explanation of that phenomenon (sexual selection via female choice). Of course, Darwin's "phenomenon in need of explanation" was an echo of the stereotype (female coyness) of the Victorian era in which he lived.

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[2] Some of her criticisms of sexual selection (e.g., the paradox of the lek) apply only to the "good genes" models, whereas others (e.g., lack of heritability of female choice in some species) apply more broadly.

[3] This is itself a confusion; the opposite of "coy" in this context is "willing to mate"; a female could be quite willing to mate, even with a number of partners, while still being choosy.

Darwin defines sexual selection as a "kind of selection" that "depends on the advantage which certain individuals have over other individuals of the same sex and species, in *exclusive relation to reproduction*" (1871 vol. I, 256; emphasis added). In this presentation of the definition, sexual selection can act on either males or females; this is one of the points of contention between Roughgarden and her critics, with Roughgarden arguing against the "extension" of "standard" sexual selection theory to females (Roughgarden and Akçay 2010). As some of the quotes below reflect, in other places Darwin characterizes sexual selection solely in terms of selection on males.

Sexual selection involves characters that are in *exclusive* relation to reproduction; sexual selection does *not*, however, involve characters that are *necessary* for reproduction. Rather, differences between the sexes that are necessary for reproduction are explained by natural selection; natural selection explains differences related to different habits of life, differences in primary sexual organs, and differences required for the care of offspring and propagation (1871 vol. I, 256). This leaves sexual selection to explain differences between sexes that are *exclusively related to reproduction* without being *necessary for reproduction*; natural selection explains all of the rest. So, the easy characterization of Darwin, "natural selection is about survival, sexual selection is about reproduction" that one sometimes sees—e.g., by one of Roughgarden's critics, Carranza (2010)—is not accurate.

Darwin acknowledges that "in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection" (1871 vol. I, 257). Note, however, that he says the *effects* are difficult to distinguish—not that there is no difference or that the effects can never be distinguished. Indeed, Darwin asserts there *is* a difference between sexual and natural selection:

> That these [secondary sexual] characters are the result of sexual and not of ordinary selection is clear, as unarmed, unornamented, or unattractive males would succeed equally well in the battle for life and in leaving a numerous progeny, if better endowed males were not present (1871 vol. I, 258).

This quote not only demonstrates that Darwin saw a difference between sexual and "ordinary" (natural) selection but also illustrates one aspect of that difference. Darwin asks us to consider the survival and reproductive abilities of males that have been favoured by sexual selection for their arms, ornaments, and attractiveness; were those males not present in the population, the males *without* those features would survive and reproduce equally well as the ones *with* those features did. The ornaments, etc., do not assist in the "battle of life" and in leaving progeny *per se*; it is only in comparison to males who are not so favoured that they offer an advantage. Indeed, Darwin maintains that such features may be "slightly injurious."

So, then, in what way can "certain individuals" have an "advantage" "over other individuals of the same sex and species, in exclusive relation to reproduction"? And what types of causes perpetuate those advantages?

Famously, Darwin characterized two kinds of "sexual struggle":

> …in the one it is between the individuals of the same sex, *generally* the male sex, in order to drive away or kill their rivals, the females remaining passive;

> whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, *generally* the females, which no longer remain passive, but select the more agreeable partners (1871 vol. II, 398; emphasis added).

In short, the two types are same-sex combat (usually male–male) where the victors are those that obtain mates, and choice of mate based on esthetic criteria (usually female choosing male). Again, contra Roughgarden, Darwin characterizes the two types in a sex-neutral manner, expressing his belief about the way things usually go while acknowledging a number of exceptions. (See 1871 vol. I, 263 for discussion of males choosing females).

The case of "monogamous" species was a bit of a puzzle. For such species, it would seem as though there would be enough females for every male to mate, regardless of the male's mating advantages or disadvantages. To account for these cases, Darwin was forced to acknowledge (what I would call) a third kind of sexual selection in which "the females,—especially the more vigorous females which would be the first to breed, [prefer] not only the more attractive but at the same time the more vigorous and victorious males" (1871 vol. II, 400). Thus, the third kind is a bit of a hybrid of the other two; females choose the attractive (and vigorous) victor. Roughgarden, however, presents this kind of sexual selection as though it were the only kind, presumably because that is the only kind of sexual selection acknowledged by many contemporary sexual selection proponents.

The "natural selection" and "sexual selection" columns of Table 1 summarize the differences between the two. Natural selection can be understood as a *causal process*, as follows: in the struggle for existence, the environment "selects" on the basis of the physical differences that give rise to organisms' differential abilities to survive and/or differential abilities with respect to characteristics necessary for reproduction. For sexual selection as a causal process, on the other hand: in the sexual struggle, organisms "select" (via esthetic mate choice, same-sex combat, or a hybrid) on the basis of the physical differences that give rise to same-sexed organisms' differential abilities to mate.[4] In both cases, "selects" should be understood metaphorically, not literally; it represents a causal interaction between the "selector" and what is "selected on."

Roughgarden's account of social selection

Roughgarden contrasts the "central narratives" of social selection and sexual selection as follows: sexual selection focuses on quantity of mating (it is "natural selection from differences in mating success"), whereas social selection focuses on quantity of offspring successfully reared—"the bottom line for evolutionary success". Social selection is "natural selection from differences in offspring-producing success".

There are two worries with Roughgarden's characterization of the central narratives: (1) it blurs the distinctions between the different types of selection, and

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[4] In principle, other views of natural selection and sexual selection can be analyzed similarly.

Table 1 Three forms of selection

	Natural selection	Sexual selection	Social selection
Type of struggle	Struggle for existence	"Sexual struggle"	Parenting struggle
Differentiation	Among conspecifics, irrespective of sex	Among members of same sex	Among members of same sex
Relevant abilities ("propensities")	Abilities to survive and/or abilities necessary for reproduction	Abilities to mate, based on characters that aid in combat or esthetic characters	Abilities to rear offspring (underlying genetic basis and organisms' development)
Selective agent	The environment, including other species	Conspecifics (esthetic mate choice, same-sex combat, or hybrid)	Conspecifics (negotiations, clique inclusions, and exclusions)

makes it harder to see what is revolutionary about social selection by hiding it under the umbrella of natural selection. (2) It focuses on differential *success*, which, as Mills and Beatty (1979) argue, risks making evolutionary theory circular; instead, we ought to focus on differential *ability*.

So, I suggest a revision: social selection involves differences in offspring-rearing *abilities*, whereas sexual selection involves differences in mating *abilities*. But what gives rise to different offspring-rearing abilities under social selection? Roughgarden's answer involves a "two-tiered" approach. The *behavioral tier* has fast, within-generation developmental changes, but no genetic changes in the population. The *evolutionary tier*, on the other hand, has slow generation-to-generation genetic changes in the population. I discuss each of these in turn, simplifying Roughgarden's presentation somewhat.

The behavioral tier uses a Nash bargaining approach to game theory. "Players" (generally pairs or small groups) negotiate the time that each spends in various offspring-rearing tasks. Possible negotiation tactics include strikes and side payments. The "game" may be played cooperatively or competitively and lead to either cooperative or competitive outcomes. Roughgarden emphasizes one of the cooperative paths to a cooperative outcome. Biologically, this involves what Roughgarden calls "team play", incorporating coordinated activity and pursuit of a common team goal: the successful rearing of offspring. However, Roughgarden acknowledges that the frequencies of competitive and cooperative paths and outcomes are an empirical matter that has yet to be fully tested.

In the evolutionary tier, payoffs for different players evolve. Traits like body size, metabolic rate, and foraging capability determine how many offspring a particular pair of genotypes can rear successfully given different distributions of their efforts. New variants of these traits will tend to increase in the population if they can, on average, increase the number of offspring that can be reared.

In short, on the social selection view (combining the two tiers), differences in genetically based traits relevant to offspring-rearing abilities give rise to different developmentally-based offspring rearing pair behaviors, probably involving team play.

But how does social selection account for secondary sexual characters? If organisms are selected for characteristics that enhance their offspring-rearing abilities, as social selection predicts, then organisms—both males and females—will be heavily invested in activities such as protecting territories and controlling resources. Depending on resource distribution, it may be advantageous for them to form "cliques"—groups within a species that control access to these resources. They may as a consequence develop "ornaments" (secondary sexual characters), such as peacock's tails or branched antlers, which may be of one of two kinds: (1) genetically based "bids" to enter a clique or (2) developmentally based "badges" to show that the organisms are members of the clique (badges develop as a consequence of access to resources). Thus, social selection provides an alternative explanation of the evolution of ornaments. (Of course, Roughgarden intends social selection to explain other phenomena that contemporary sexual selection proponents have sought to explain—e.g., origin of sexual reproduction and of the male/female binary).

The "sexual selection" and "social selection" columns of Table 1 summarize the differences between the two. Social selection can thus be understood as a causal process as follows: In the parenting struggle, organisms "select" (through their negotiations and though clique inclusions and exclusions) on the basis of the physical differences that give rise to organisms' differential abilities to rear offspring.

Summing up the causal process approach

Natural selection, sexual selection, and social selection each posit a different area of "struggle". Natural selection occurs with respect to any differences among members of the same species, whereas sexual selection and social selection occur with respect to differences among members of the same sex. More specifically, natural selection acts on differences in survival and reproductive abilities, sexual selection acts on differences in mating abilities, and social selection acts on differences in offspring-rearing abilities. For natural selection, the environment "selects" on the relevant differential abilities; for sexual and social selection, organisms "select" on the relevant differential abilities, with sexual and social selection differing in the ways in which organisms select (as above). (There are also some differences in expected outcomes, which I lack space to discuss).

Of course, in principle, one could use natural selection as an umbrella term while recognizing that it is a cover for different sorts of causal processes, since what is most important is the recognition that there *are* different types of causal processes. However, using different terms for the different causal processes helps ensure that none of them are overlooked, forcing us to make explicit which are operating and to what extent.

There are three general implications of the causal process approach: (1) We can see how sexual selection and social selection pertain to a different domain than natural selection and the extent to which they offer competing accounts of that domain. (2) We can see the different kinds of biological phenomena that are lumped together if natural selection is simply differences in reproductive success due to heritable fitness differences. (3) We ought to be measuring and tracking the various abilities (survival, reproduction, mating, offspring rearing—and perhaps others), rather than "fitness" simpliciter.

In short, Roughgarden is vindicated in offering a revolutionary alternative to sexual selection and not a mere revision to existing views. And Darwin is vindicated in his separation of natural selection from sexual selection.[5]

Angela Potochnik

The primary purpose of *The Genial Gene* is to criticize the many individual hypotheses grouped under the rubric of sexual selection theory and to develop alternative hypotheses that account for the traits in question. Roughgarden identifies 26 empirical hypotheses, on issues ranging from the evolution of sexual reproduction and sexual dimorphism to the behavioral ecology of mating, reproduction, and the rearing of young (237–238). Together, these comprise the empirical content of social selection theory.

Yet, the empirical hypotheses are not the entirety of the project. Roughgarden's first sentence declares that "this book is about whether selfishness and individuality, rather than kindness and cooperation, are basic to biological nature" (1). My aim here is to establish the role that this claim plays in Roughgarden's research program. The broad-scope theoretical claim that cooperation is basic plays a fundamental and intriguing role in Roughgarden's project. Understanding that role uncovers an important element of Roughgarden's criticism of sexual selection theory. It also is key to understanding the nature of Roughgarden's dissatisfaction with other accounts of the evolution of cooperation.

Debunking selfishness

Roughgarden's claim that kindness and cooperation are basic to biological nature is more than an opening line; it plays an important role in her project. What to make of that role is part of what is at issue between Roughgarden and sexual selection theorists. It is also a non-trivial part of understanding social selection theory. In this section, I critically examine how Roughgarden's ideas about the basics of biological nature contribute to her research program.

Near the end of the book, there is a brief argument for the rejection of sexual selection theory in its entirety. Roughgarden asks the reader to "consider the implications of sexual selection being incorrect on all 26 [empirical hypotheses]" (247). She argues that, if the sexual selection hypotheses were mutually independent, the chances that they *all* would be wrong are vanishingly small. She concludes that, instead,

> some feature common to all 26 propositions in sexual selection must exist to explain why they are all incorrect at the same time. That feature is that all 26 points derive from a common view of natural behavior predicated on selfishness, deception, and genetic weeding. If this view of biological nature is

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[5] Thanks to the Roughgarden Lab at Stanford University and the Griesemer/Millstein Lab at UC Davis for helpful discussion. Thanks are also owed to Erika Milam, Angela Potochnik, and Joan Roughgarden for an enjoyable session at ISHPSSB 2009.

> wrong, then deriving any 27th or 28th additional element for [the sexual selection system] will fail as well. Thus, the sexual selection system cannot be somehow repaired or sanitized. Its foundation is incorrect (247).

Roughgarden claims that sexual selection theory is a codification of the view that selfishness etc. characterizes the evolved traits related to gender, sex, and reproduction. In this passage, she suggests both that the view that selfishness is basic influences the nature of sexual selection hypotheses and that the incorrectness of those hypotheses indicates that the belief that selfishness is basic is false.

Let us consider these two ideas individually. According to the first, a view about what is biologically basic influences the empirical hypotheses that are generated. It is clear that broad-scope beliefs play this role for Roughgarden's social selection theory—namely, the belief that kindness and cooperation are commonplace in the living world. For example, Roughgarden (2004) initially conceded that the peacock's colorful train fits within the sexual selection framework. Takahashi et al.'s (2008) empirical findings against the role of this train in mate selection led Roughgarden to reconsider. Her view that cooperation is commonplace in the animal kingdom then sparked the hypothesis that the peacock's train fits into that rubric: perhaps social dynamics, not sexual dynamics, give a colorful train its value. Empirical findings against the female mate-choice hypothesis occasioned this new hypothesis, and empirical findings will decide the success of Roughgarden's replacement hypothesis. But the formulation of the new hypothesis was surely influenced by antecedent views about the character of the living world.

In Roughgarden's view, sexual selection theory is similarly guided by a commitment to selfishness. If so, that commitment is generally left unarticulated by sexual selection advocates. Yet, broad-scope beliefs of some sort do play a role in sexual selection theory. In response to challenges to some sexual selection hypotheses, Clutton-Brock (2007) responds that "the theory of sexual selection still provides a robust framework that explains much of the variation in the development of secondary sexual characters in males." One role of sexual selection theory is as a framework that guides the formulation of individual empirical hypotheses, much as an explicit commitment to cooperation guides Roughgarden's hypotheses.

Yet, Roughgarden risks overstating the connection between background views and empirical hypotheses. A view of what is basic to biological nature cannot issue direct predictions about the living world. Even if kindness and cooperation are basic, there is a great deal of latitude in how kindness/cooperation is manifested, as Roughgarden (2004) amply demonstrates. Additionally, views of what is basic to biological nature not only accommodate a variety of manifestations in the living world but also allow occasional departures from the pattern. Roughgarden allows that some behaviors may be best described in terms of conflict, and Clutton-Brock (2007) allows for instances of mating behavior that do not conform to the pattern of female choice. A view about what is basic can inspire empirical hypotheses, but it certainly does not entail them.

The second relationship that Roughgarden posits between the view that selfishness is basic and sexual selection theory runs in the opposite direction. She claims that demonstrating that the empirical hypotheses of sexual selection are incorrect *falsifies* the view that selfishness is basic to biological nature. Surely, this is wrong. Even assuming that the empirical hypotheses in question are motivated by the view that sexual behavior is based on "selfishness, deception and genetic weeding," the failure of those hypotheses does not wholly undermine this view of biological nature. I have argued that a claim about what is biologically basic does not prescribe particular empirical hypotheses but is consistent with a variety of hypotheses. Accordingly, the failure of any number of empirical hypotheses cannot falsify a view of the basics.

Disconfirmation of any sort seems the wrong way to think about the relationship between empirical claims and broad-scope claims about what is basic. If the latter does not issue specific predictions, then it is not directly subject to confirmation or refutation. A view of what is basic to biological nature is better seen as a guiding heuristic, judged according to its fruitfulness rather than its truth. The connection between empirical observations and a claim that, e.g., selfishness is biologically basic is heavily attenuated. Selfishness may be defined in any number of ways for a wide variety of phenomena. It is also unclear what range of influence to expect from a quality dubbed basic. The scientific value of a view about what is biologically basic is its ability to inspire novel empirical claims, claims that *can* be confirmed or disconfirmed.

This idea is supported by points made above. A view of what is basic to biological nature is compatible with any specific empirical outcomes, indeed, can engender an array of distinct hypotheses for a single phenomenon. Consider also the relationship among empirical hypotheses inspired by some view of the basics. Only for closely related phenomena can the accuracy of a hypothesis for one phenomenon provide evidence of its accuracy for another. For instance, if a rich cooperative social network is discovered in one species of birds, this is some evidence for similar networks in other species. Expectations for similar dynamics in substantively similar evolutionary outcomes are based on more than broad claims about what is basic to nature. In contrast, the success of hypotheses for more disparate phenomena is virtually independent. The cooperative rearing of young in birds gives no evidence that anisogamy (the egg/sperm binary) evolved for mutual advantage, even if both hypotheses result from the view that cooperation is basic to biological nature.

Sexual selection hypotheses about the evolution of sex, gender, and reproduction succeed or fail individually, as relatively independent claims about evolution. The same is true for Roughgarden's competing empirical hypotheses. A commitment to the view that kindness and cooperation are basic does not warrant accepting those hypotheses, nor does the rejection of that view warrant rejecting those hypotheses. Some evolutionary outcomes are best described in terms of conflict (203), but this alone does not undermine the claim that cooperation is "basic." Similarly, the success of social selection theory would not falsify, or even disconfirm, the idea that selfishness is basic. Empirical claims about the world do not proceed in lockstep with a view of what is basic.

However, a view of what is biologically basic is not entirely beyond the purview of empirical results. If, as I suggested, a view of the basics should be judged for its fruitfulness, then an unfruitful view of the basics should be jettisoned. The debate over social selection theory includes a disagreement on precisely this point. Each side accuses the other of imposing a favored worldview that is not reflected in the living world. Coyne (2004), in a review of Roughgarden (2004), claims that "[Roughgarden's] agenda… is explicit and ideological." Roughgarden responds in kind. She says, "Neo-Spencerists have not scientifically demonstrated their world view of nature. They have merely stipulated it and ridicule any alternative view of nature as romantic wishful thinking" (3). Each posits that one view of what is biologically basic generates plausible empirical hypotheses about gender, sex, and reproduction and that the competing view is imposed as an interpretation—a *mis*interpretation—of those traits. This can be viewed as a disagreement over the fruitfulness of different views of the basics.

In summary, Roughgarden's insistence that her book is about what is "basic to biological nature" is not empty rhetoric. Her criticisms of sexual selection theory are partly inspired by her commitment to the roles of kindness and cooperation, and the points of dispute include the role played by competing broad-scope commitments. Roughgarden's work exemplifies the socially engaged science proposed by Longino (1990). Yet, Roughgarden's claim that she has falsified the view that selfishness is basic is incorrect. Instead, the success of her criticisms should be judged by whether she has demonstrated that selfishness and deceit are common evolutionary hypotheses not because they are commonplace in the living world, but because of a misguided theoretical commitment. Roughgarden should not aim to falsify a commitment to selfishness but to demonstrate its unfruitfulness.

Accounting for cooperation

Roughgarden distances her approach from other attempts to account for cooperation in nature. She is critical of accounts of the evolution of altruism in terms of group selection, reciprocal altruism, or kin selection. Given her emphasis on cooperation, it is initially a bit mystifying why Roughgarden regards these models for the emergence of cooperative behavior as foes instead of friends. Here too, her broad-scope claim that cooperation is basic is at the heart of her criticisms.

Roughgarden's primary criticism of kin selection and reciprocal altruism is that both "are theories whose purpose… is to take the altruism out of altruism—theories that devise a way to see how cooperative behavior is really deep-down selfishness after all" (3). These theories account for cooperation by showing how cooperative behavior leads to advantage at the level of genetic inclusive fitness (kin selection) or as a product of repeated interactions (reciprocal altruism). An advocate of the "selfish gene" view may construe this as selective advantage as the product of selfishness, either at the genetic or at the individual level (12). This makes cooperation illusory, thereby violating Roughgarden's commitment to cooperation as basic.

Roughgarden's contention against group selection is that, though theoretically possible, the differential success of groups is not common. Behavior, even social behavior, leads to fitness consequences for individuals (12). Roughgarden's concern seems to be that group-selection models assume that individual-level selection acts against cooperative behavior and is counteracted only by group-level selection for cooperation. Again, cooperation is taken to be non-basic. In contrast, Roughgarden expects that "ordinary individual-level natural selection" often favors cooperation (186). No special appeal to a different level of advantage is needed; cooperation simply pays off.

Here, Roughgarden's criticisms of approaches to accounting for cooperation converge. Roughgarden notes that kin selection models and group-selection models are mathematically equivalent (e.g., Kerr and Godfrey-Smith 2002) and that both represent selection acting in opposed directions. Group-selection models represent individual-level selection against cooperation and group-level selection for cooperation. Kin selection models incorporate into a gene's inclusive fitness the fitness cost to gene copies in benefactors and the fitness benefit to gene copies in beneficiaries. Both assume cooperation has a cost. In contrast, Roughgarden's commitment to cooperation as basic leads to the expectation that cooperation often results in direct selective advantage (185–186).

In the levels of selection debate, altruistic behavior is commonly defined as behavior that benefits others at a personal fitness cost (Sober and Wilson 1998). This suggests that any behavior that benefits the actor is selfish, a definition that Roughgarden criticizes. Choosing this dividing line between selfishness and altruism makes selfishness the evolutionary default: any behavior that results in individual selective advantage is, by definition, selfish. Any account of the evolution of cooperation that employs this definition of selfishness—including kin selection, reciprocal altruism, and group selection—prejudges the question of what is basic to biological nature.

Roughgarden suggests an alternate definition of cooperation that does not equate direct fitness advantage with selfishness. She argues that models of social behavior should explicitly represent both (1) how behavior develops during the life span of individuals and (2) how behavioral strategies evolve through evolutionary time. Then, cooperation can be defined in terms of behavioral dynamics, rather than simply selection dynamics. As Roughgarden et al. put the point,

> The distinction between our proposition and previous work is apparent in the use of the word cooperative, which means only a mutually beneficial outcome in previous work but describes a process of perceiving and playing the game in our work (2006, 967).

Defined in terms of behavioral dynamics, cooperation need not involve a cost to direct fitness. Instead, cooperation is defined by how social interactions are approached. For example,

> through reciprocal calls and physical intimacy, players perceive team fitness and act accordingly rather than play solely as individuals. Communication during courtship permits bargaining and promises of side payments (2006, 966–967).

In this scenario, individuals have recourse to bargaining, side payments, and threat points to ensure mutually advantageous arrangements. Yet, the arrangement qualifies as cooperative, for social behavior is employed to accomplish mutual advantage.

In Roughgarden's view, other approaches err in the assumption that cooperation cannot be directly advantageous. Those approaches assume either that cooperation comes about through a separate form of selective advantage (group fitness or inclusive fitness) or that cooperation is at root selfishness (reciprocal altruism). In contrast, Roughgarden claims that "many instances of cooperative behavior are best explained as the kind of team play envisioned in our behavioral tier, combined with ordinary individual-level natural selection in the evolutionary tier" (186). She thinks that once cooperation is adequately defined, it is not an evolutionary enigma, but a common successful strategy.

This is another role played by the commitment to kindness and cooperation as basic. Eliminating the assumption that individual advantage simply *is* selfishness creates room for the hypothesis that cooperation emerges via individual selective advantage. Yet, this brings to the fore another difficulty with how Roughgarden wields her broad-scope theoretical claims. Notice that Roughgarden's preferred definition of cooperation applies only to social behavior, to organisms that have the potential to engage in team play. This is not relevant to some traits Roughgarden deems cooperative. For instance, she postulates that anisogamy is due to mutual advantage rather than sexual conflict. But if the physical trait of gamete size is to count as a cooperative outcome, the definition of cooperation must be altered to include non-behavioral traits. The behavioral sense of cooperation is not broad enough to be basic to biological nature.

This illustrates how different conceptions of the basics may lead to an overemphasis of differences. Roughgarden's criticism that group selection and kin selection are not common evolutionary mechanisms is an empirical disagreement with advocates of those views. In contrast, her criticism that group selection, kin selection, and reciprocal altruism consider all individually advantageous behavior to be selfish is a dispute about words rather than the world—it hinges on the definition of "selfishness". Roughgarden's criticism on this point does not preclude the possibility of, e.g., successful reciprocal altruism models. It simply allows for disagreement over whether the behavior in question should be considered selfish.

If Roughgarden is right that flawed evolutionary explanations result from the assumption of widespread selfishness, perhaps the proper lesson is not to assume widespread cooperation, but to avoid committing to *any* view of what is basic to biological nature. The success of Roughgarden's empirical hypotheses will likely vary from case to case; as Roughgarden readily acknowledges, much empirical work remains. The extent of empirical differences is also yet to be determined. The danger of any wholesale commitment to what is basic to nature is that it may obscure failures of the favored theory and empirical equivalences with other theories. Perhaps the true value of the claim that cooperation is basic is in its power to undermine implicit assumptions of the opposite.[6]

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[6] Thanks to Joan Roughgarden, Roberta Millstein, Erika Milam, Erol Akçay, and Pria Iyer for helpful discussion and to Sarah Richardson for useful comments on an earlier draft.

Author's response: Joan E. Roughgarden

To Erika Milam

I thank Erika Milam for her analysis of the historical context of *The Genial Gene* and for her appreciation of how the book may advance our understanding of the evolution of social behavior. I address now her primary critical points.

Milam argues that my theory of social selection is not a replacement of sexual selection, but a special rendition of sexual selection that accords with writings in the 1960s by *Drosophila* population geneticists such as Dobzhansky (1955), Petit (1958), and Ehrman (1970) and the avian population geneticist O'Donald (1980), among others. I accept that my perspective on the evolution of social behavior, with its emphasis on the naturalness and value of genetic diversity, is more consonant with those population-genetic workers of the 1960s than it is with later, largely sociobiological writers in the 1970s such as Dawkins (1976), Hamilton (1964), Trivers (1972), Parker (1979), among others.

Even though, as Milam points out, social selection might be seen as a form of what sexual selection was thought to be by some during the 1960s and earlier, it does differ from what sexual selection is understood to be today. I contend that today's sexual selection is basically the same as what Darwin was describing, and I claim that sexual selection in both Darwin's and today's sense is empirically unsubstantiated and theoretically problematic. Therefore, social selection, in differing from today's sexual selection, can qualify as a replacement for sexual selection, providing it is eventually verified in future empirical and theoretical research.

To see that Darwin's vision of sexual selection is essentially the same as today's sexual selection, let us simply inspect what both Darwin wrote and what a contemporary geneticist writes and compare.

Darwin (1981) wrote, "Males of almost all animals have stronger passions than females", and "the female… with the rarest of exceptions is less eager than the male… she is coy". These "coy" females choose mates who are either beautiful or well armed, or both: "Many female progenitors of the peacock must… have… by the continued preference of the most beautiful males, rendered the peacock the most splendid of living birds". Similarly, female preference for victorious males caused males to become "vigorous and well-armed… just as man can improve the breed of his game-cocks by the selection of those birds, which are victorious in the cock-pit". All in all, males evolve to be beautiful and well armed, because of female mate choice.

The geneticist Jerry Coyne (2004) wrote, "We now understand… Males, who can produce many offspring with only minimal investment, spread their genes most effectively by mating promiscuously… Female reproductive output is far more constrained by the metabolic costs of producing eggs or offspring, and thus a female's interests are served more by mate quality than by mate quantity".

Coyne's present-day narrative is identical to Darwin's, excepting that passionate male has become promiscuous male and coy female has become constrained female. That is, passionate/promiscuous males with cheap sperm are constantly searching for chances to mate, and coy/constrained females with expensive eggs ascertain which males have the best ornaments or armaments/genes.

In both Darwin's and Coyne's narrative, the males can be objectively ranked in terms of heritable quality and females try to identify the highest male in the quality hierarchy and settle for whom they can get. This is precisely the narrative taught today as established fact in standard college biology curricula and textbooks.

I claim that this story simply does not take place in nature. There are no regularities of the sort Darwin claimed—females are not generally coy nor males generally more passionate than females, sperm is not generally cheap, females are not often constrained by their eggs, nor do they ever bother to select mates on the basis of genetic quality, and no hierarchy of genetic quality exists among males, and so forth. The whole story is nothing but a tall tale.

Moreover, the standard sexual selection story does not make theoretical sense when carefully considered because of the "paradox of the lek" (impossibility of maintaining a continuous supply of bad genes to sustain female choice for continued genetic weeding) and the inability of animals ever to discern minuscule fitness differences that result from differences in the number of weakly deleterious mutations accumulated by different individuals.

I suggest something else altogether is going on. Females are choosing mates to maximize offspring number, not genetic quality; males indeed care about successful rearing of offspring for otherwise their expensive sperm will have been cast to the wind. And so on. *The Genial Gene* develops an extensive account of what is happening in reproductive social behavior that point by point differs from what today's sexual selection, or its extensions, envision. In this sense, it is correct, I believe, to assert that social selection is an alternative and potentially a replacement for sexual selection.

Milam argues that the primary importance of social selection lies in how it "is part of a much larger project, a radical re-envisioning of the evolution of social behavior in animals based on an acceptance of the complexity of animal mind that has become current only in the last decade or so". She discounts the importance of contrasting social selection with sexual selection. I accept that social selection is indeed a re-envisioning of social evolution that awards to animals sophistication in decision making that goes far beyond what would have seemed plausible several decades ago when the work of Lorenz (1937), Skinner (1938), and Tinbergen (1951) was current. And she may indeed be right that discussions of the contrast between social selection and sexual selection may turn out in the long run to be less important than discussion of the implications for how social selection offers a theory for the evolution of social behavior that incorporates a "reinvigorated view of animal mind" as it develops a "new set of analytical tools".

To Roberta Millstein

I thank Roberta Millstein for providing helpful clarification of the distinctions among natural selection, sexual selection, and social selection and for her defense of how social selection can be seen as new and revolutionary proposal in light of a causal analysis of the processes that produce these three forms of selection. I turn now to the points of disagreement.

Millstein observes that sexual selection suffers from a multiplicity of definitions and models, many of which are inconsistent with one another. A confusion about exactly what sexual selection means unfortunately is present in Darwin's original writings on the topic. Attempts at divining what Darwin really meant can resemble a psychic trying to speak with the dead. On the one hand, in a single passage, Darwin offers what might seem to be a clear generic definition: sexual selection is a "kind of selection" that "depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction". On the other hand, in many passages, Darwin characterizes sexual selection in terms of highly gendered mating strategies. Millstein notes that Darwin has three references to females being coy and requiring courtship, whereas I would add that his generic definition occurs in only one passage. And Millstein acknowledges that Darwin frequently writes, and evidently believed, that in general females are coy and males eager, with the "rarest of exceptions". Still, Millstein does not think the stereotypical sex roles are Darwin's central focus. The blame for emphasis on the stereotypical sex roles should instead be placed with later readers of Darwin. And Millstein claims that coyness is a phenomenon to be explained by sexual selection theory, not part of the theory itself. Well, I do not see it. I see no reason to let Darwin off the hook on this matter, pinning the blame on later workers. Female coyness is indeed a central part of Darwin's theory because females are primarily doing the mate choosing and, in doing so, inherently can be accused of seeming coy and requiring of courtship while they accumulate the experience and evidence upon which to make their choice.

Similarly, Millstein wants to excuse Darwin from responsibility for a gendered characterization of the "sexual struggle". She acknowledges that same-sex combat is intended to refer to male–male combat and that mate choice based on esthetic criteria is intended for female choice of males but says that Darwin nonetheless described the sexual struggle in a sex-neutral manner. Not really. Although Darwin is aware of some sex-role-reversed species, in such cases, he describes the male as acting like a female and vice versa. The phenomenon of sex-role reversal remains problematic today. And Millstein refers to female choice of armed males as a "hybrid" between same-sex combat and esthetic preference. Not so. Darwin is clear that the female esthetic is supposed to favor both ornaments and armaments, which conveniently aligns the female esthetic with victory in male–male combat. In my opinion, the best tribute to Darwin is say up front when he is right and when he is wrong and not to cast his writings in a way to make him appear always correct. I appreciate that Professor Millstein and I have an honest disagreement about how Darwin is to be read. Yet, from my perspective, I find it hard to locate Millstein's interpretation outside the industry of Darwinian apologia occasioned by recent anniversary celebrations of Darwin's publications.

Anyway, all this discussion of what Darwin really meant is beside the point of how to distinguish natural selection from sexual selection from social selection, which I think is the main value of Millstein's contribution. As Millstein notes, most biologists today use "natural selection" as an umbrella term that subsumes the many ways in which natural selection occurs. We will need two words then. What we might term “wide-sense natural selection” is today’s umbrella-natural selection, and “narrow-sense natural selection” is the natural selection that Darwin was distinguishing from sexual selection, as Millstein details in the first column of her Table 1.

I accept Millstein’s account of social selection and think that the columns of Table 1 offer a marvelously clear distinction among (narrow-sense) natural selection, sexual selection, and social selection. I also accept Millstein’s suggestion that my use of the word “success”, as in “success in parenting”, should be replaced by the word “ability”, rendering the phrase as “ability in parenting” to avoid any slippage into circularity.

I think that Millstein’s introduction of causal process analysis to the discussion of sexual selection is an important clarifying innovation. I look forward to seeing the approach extended to certain other “types” of selection discussed in the evolutionary literature, such as *r*-selection and *K*-selection, by augmenting Millstein’s Table 1 with additional columns.

To Angela Potochnik

I thank Angela Potochnik for engaging what I feel is the most important philosophical issue to be raised by *The Genial Gene*, namely the epistemological status of general claims about the basics of biological nature. Of all the reviews and commentaries that the book has received, Potochnik’s contribution is the first to consider what it means to hold a position on the general character of biological nature, including, by extension, our own human nature.

Potochnik’s view of the epistemological status of general claims about biological nature is that they are guiding heuristics, not truth claims. She writes, “what is basic to biological nature is better seen as a guiding heuristic, judged according to its fruitfulness rather than its truth”. As such, “A view about what is basic can inspire empirical hypotheses, but it certainly does not entail them”. And again, “A view of what is basic to biological nature cannot issue direct predictions about the living world”. Hence, “a view of the basics should be judged for its fruitfulness” not its truth. Thus, “Roughgarden’s claim that she has falsified the view that selfishness is basic is incorrect” and “Roughgarden should not aim to falsify a commitment to selfishness, but to demonstrate its unfruitfulness”.

Obviously, I completely disagree with Potochnik concerning the epistemological status of general claims about biological nature. My position is that such claims are neither heuristics nor merely metaphors but are indeed offered as universal empirical claims about nature. My position is that such claims do formally entail, as a matter of logic, certain predictions, that such claims can therefore be logically falsified by falsifying their consequents, and that such claims do have truth value and thus may be determined as true or false through empirical investigation.

How would one settle the disagreement between Potochnik’s and my view of the status of selfishness as a general characteristic of biological nature? I suggest we consult how the premise that biological nature is founded on selfishness is used. I quote at length from David Beldon (2009) who reviewed *The Genial Gene* for a lay audience in the magazine *Tikkun*. Beldon writes, “I still have my 1978 paperback edition of Richard Dawkins's *The Selfish Gene*… Two of my best friends, animal behaviorists, gave it to me to explain their world… Altruism is just a variety of selfishness. I was persuaded by my expert friends' certainty as well as by Dawkins's logic… [that] to build a culture based on unselfish values, we have to be aware of our selfish genes and deal with them. This is the conclusion I drew after reading Dawkins. The carpenter cannot create a functional and beautiful staircase if she doesn't know the wood: working against the grain just creates a mess". This quote indicates that at least some people, I suspect a very great many, think that the phrase, "selfish gene" refers to a universal state of nature that we must be aware of and contend with. The phrase is taken as referring to a *fact* of nature, unlike say, the phrases, "life is tough", or "keep a happy face", both with possible heuristic value that one would not think of trying to falsify.

Not only has the educated lay public been told on behalf of evolutionary biology that biological nature is selfish, scientists too use the notion of selfishness as a working premise. Godfray (2005), writing about parent–offspring conflict in the "Quick Guide" section of the journal, *Current Biology*, admonishes the reader to think in terms of selfish genes. Godfray says rhetorically, to the reader, "you are viewing evolution in terms of the fitness of individuals rather than genes. Most of the time it makes no difference but this [parent-offspring conflict] is one of the situations where an explicit gene's-eye view is essential. The selfish gene [leading to parent-offspring conflict] spreads because it does better than alternative 'non-selfish' alleles at the same locus".

Indeed, the topic of parent–offspring conflict nicely illustrates how the notion of selfishness in biological nature entails specific predictions. Assume two chicks are calling for food from a parent. On the one hand, assume nature is selfish. Then, the chicks' calling is intended to manipulate the parent into providing more food than is in the parent's own best interest (parent–offspring conflict) and is intended to manipulate the parent into giving each chick food that the other chick needs (sib–sib conflict). On the other hand, assume nature is cooperative. Then, the chicks are honestly signaling their need. The parent can adjust food distribution to guarantee that the chicks are awarded food, each according to its need, to maximize the family prosperity.

The issue here is not which is correct; the point is different predictions about the honesty of the chicks' signaling are entailed by the assumptions of selfishness and cooperativeness. And indeed, evidence that the chicks do signal honestly has required developing the theory of costly signaling as a way of reconciling the chicks' honesty with the assumption of selfishness. Potochnik argues that "a claim about what is biologically basic does not prescribe particular empirical hypotheses". To the contrary, the assumption of selfishness *does* entail when accompanied with particularizing assumptions, specific predictions. Therefore, viewing general claims about selfishness as subject to "disconfirmation", and indeed, to empirical falsification, is entirely appropriate.

Moreover, if one prediction after another that relies on selfishness is found to be incorrect, a full 26 are enumerated in *The Genial Gene*, then eventually the assumption of selfishness itself draws suspicion, rather than one of the many particularizing assumptions that also participate in deriving specific predictions.

Sexual selection hypotheses are clearly not a collection of "relatively independent claims about evolution" as Potochnik asserts but are a carefully woven tapestry of explanation for a cluster of related phenomena all pertaining to reproduction, sex, gender, and sexuality. This entire tapestry is falsifiable, indeed actually false, in my judgment. Although Potochnik wishes to assess sexual selection and social selection in terms of whether they are fruitful, rather than whether they are true, it is difficult to see how a false scientific theory could be considered fruitful. Even though we can all applaud the role sexual selection theories have had in stimulating discussion and leading to academic employment, their political and economic fruitfulness is irrelevant to the final assessment of scientific fruitfulness.

In defense of Dawkins (1976), Ruse (2009) has complained that my criticism of the selfish gene concept is unfair because the selfish gene is merely a metaphor. Ruse does not understand that over the last nearly 40 years, the selfish gene has been promoted from its standing as a clever turn of phrase, perhaps a metaphor, to a statement about basic biological nature. My point is that the universal selfishness alluded to by the phrase, selfish gene, does not in fact occur, and I offer as evidence that all predictions derived from that premise fail under empirical examination. Instead, the data would seem more to support a universal degree of cooperation in nature.

Potochnik's commentary is also the first to appreciate the distinction in *The Genial Gene* between how cooperation evolves by team play rather than by kin/group/multilevel selection as traditionally assumed in evolutionary biology. Potochnik writes,

> Group selection models represent individual-level selection against cooperation and group-level selection for cooperation, while kin selection models incorporate into a gene's inclusive fitness the fitness cost to gene-copies in benefactors and the fitness benefit to gene-copies in beneficiaries. Both assume cooperation has a cost. In contrast, Roughgarden's commitment to cooperation as basic leads her to expect that cooperation often results in direct selective advantage…. Defined in terms of behavioral dynamics, cooperation need not involve a cost to direct fitness. Instead, cooperation is defined by how social interactions are approached.

Potochnik's clear understanding of team-play contrasts with the confusion of Okasha et al. (2009) who try to force the idea of team play into their own group-selection framework, even though team play obviously does not involve opposing selection at two levels (multilevel selection). Okasha et al. (2009) write, "certain aspects of Roughgarden's own theory seem conceptually close to group selection, in particular her idea that in common-interest interactions, pairs of animals try to maximise a 'team fitness function'". This misunderstanding is disappointing in view of the clear distinction between two-tier models of *The Genial Gene* in which the lower tier is not a selection process at all but consists of within-generation behavioral or developmental dynamics, and only the upper tier features a selection process. *The Genial Gene*'s two-tier formulation is more in the spirit of "evo/devo" models in which the lower level consists of developmental dynamics and the higher level consists of evolutionary dynamics, than of multilevel selection models.

Potochnik does a service in clarifying this distinction between two-tier and multilevel models and in showing how adopting a two-tier framing for the evolution of cooperation does away with the requirement of assuming that cooperation (or altruism) is inherently opposed by natural selection so that it must be supported by counter selection at some higher level. Instead, through team play, a cooperating individual directly benefits from their cooperative behavior, and the trait for cooperation can therefore evolve by ordinary natural selection.[7]

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