

# Joan Roughgarden

## *Challenging Darwin's theory of sexual selection*

May a biologist in these polarized times dare suggest that Darwin is a bit wrong about anything? Even worse, does a biologist risk insult, ridicule, anger, and intimidation to suggest that Darwin is incorrect on a big issue? We have a test case before us. Darwin appears completely mistaken in his theory of sex roles, a subject called the 'theory of sexual selection.'<sup>1</sup>

In his 1871 book *The Descent of Man, and Selection in Relation to Sex*, Darwin 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."<sup>2</sup> Notice that the exceptions are dismissed as empirically insignificant

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("almost all," "rarest of exceptions"), so that, for all practical purposes, males are universally "passionate" and females collectively "coy."

To explain this claim, Darwin considered the joint mechanisms of male-male competition and female choice. He envisioned that males compete for access to females, while females choose superior males on the basis of success in male-male competition and/or perceived beauty. In effect, through their choice of mates, females breed their offspring to have their mates' desirable traits, "just as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cockpit." Another example: "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." From a masculinist perspective, acquisition of females is a just reward for victory in male-male combat. From a maternalist perspective, the duty of females is to bed

1 J. Roughgarden, *Evolution's Rainbow: Diversity, Gender and Sexuality in Nature and People* (Berkeley: University of California Press, 2004).

2 C. Darwin, *The Descent of Man, and Selection in Relation to Sex*, facsimile edition (Princeton, N.J.: Princeton University Press, 1871).

the victors, thus endowing their offspring with valuable traits.

The Darwinian narrative of sex roles is not some quaint anachronism. Restated in today's biological jargon, the narrative is considered proven scientific fact. The geneticist Jerry Coyne, at the University of Chicago, declared: "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."<sup>3</sup> So the passionate male has become the promiscuous male, and the coy female the constrained female. Yet the spirit of this present-day narrative is identical to Darwin's of nearly 130 years ago, and the sexual conflict that flows from attributing different objectives to males and females remains the starting point for sexual-selection theory today just as it did in Darwin's time.

I have been foolhardy enough to suggest that this thoroughly entrenched theory of male-female relationships is biologically mistaken. The response to my proposal offers a revealing commentary on the willingness of evolutionary biologists to face up to contrary evidence and logic. Let us turn to the proposal and then to the responses.<sup>4</sup>

3 J. Coyne, "Charm Schools," *Times Literary Supplement*, July 30, 2004.

4 The following exposition of the proposal is condensed from a recent review, which should be consulted for further detail and references to primary literature: J. Roughgarden, "Social Selection vs. Sexual Selection: Comparison of Hypotheses," in Daniel Kleinman and Jo Handelsman, eds., *Controversies in Science and Technology*, vol. 2, *Genetics of Race and Gender* (Madison: University of Wisconsin Press, 2007).

I refer to sexual selection today as a *system*, meaning a set of logically interconnected theoretical propositions with a truth status independent of the facts they were originally intended to explain. As contrary data appear, the theoretical propositions are updated. Thus the system cannot be challenged and becomes, in effect, tautological.

By using the word system, I also echo the phrase "sex-gender system," coined in 1974 by the anthropologist and gender theorist Gayle Rubin.<sup>5</sup> Rubin emphasized how expectations flowing from how a culture defines gender wind up "the part of social life which is the locus of the oppression of women, of sexual minorities." Although gender categories may not be constructed for the purpose of oppressing others, they end up authorizing such oppression by defining what counts as a norm and what counts as an exception, thereby privileging one over the other.

In place of sexual selection, I propose social selection. It is equally extensive but differs point by point from sexual selection. Social selection is selection for, and in the context of, the social infrastructure of a species within which offspring are produced and reared. The social strategies in the infrastructure generally include cooperation as much as – or more than – they do competition; and they revolve more around negotiation than 'winning.' Social selection, in my formulation, does not extend sexual selection but replaces it.

Ultimately, the evolutionary system of sex, gender, and sexuality that prevails determines our worldview of nature itself. Sexual selection's view of nature emphasizes conflict, deceit, and dirty

5 Gayle Rubin, "A Contribution to the Critique of the Political Economy of Sex and Gender," *Dissemination* 1 (1) (1974): 6–13; 1 (2) (1974): 23–32.

gene pools. If this Darwinian picture of nature is true, so be it. But is it true?

To begin with, sexual selection and social selection differ in their accounts of the very origin of sexual reproduction and the sexes.

*Origin of sexual reproduction.* According to sexual selection, sexual reproduction evolved from asexual reproduction as a mechanism to cleanse the gene pool of deleterious mutations. According to social selection, sexual reproduction evolved from asexual reproduction to maintain a diverse gene pool needed for long-term population survival in an ever-fluctuating environment.

*Origin of gametic male/female binary.* The difference in size between the sperm and the egg is the basis for defining male and female in a sexually reproducing species. Sexual selection imagines the protosperm and protoegg playing a game against each other. Initially, both the protosperm and protoegg are the same size. But then the protosperm ‘cheats,’ becoming a little smaller so that more sperm can be produced with the leftover energy. This numerical advantage allows the smaller sperm to outcompete the less numerous sperm of the original size. The protoegg responds by increasing its size, restoring zygote viability to its original level. This compensating move is better than shrinking to try to match the smaller sperm; otherwise, the zygote would suffer a very deleterious double loss of investment. These responses of egg and sperm to each other culminate in one gamete – the protoegg – growing nearly as large as the zygote, and the other – the protosperm – becoming as tiny as possible.

In sexual selection, the distinction between male and female gametes arises from a battle: the sexes are created as combatants. But according to social se-

lection, a parent divides the material it places into eggs and sperm to maximize the number of *gametic contacts* that produce viable zygotes. The number of gametic contacts increases as gametes become more numerous and form a large, dense cloud. The greatest number of viable zygotes is thus created when one of the gametes is close to the desired zygote size while the other is as small as possible.

*Origin of whole-organism male/female binary.* If a sexually reproducing species produces more than one type of gamete, each individual of that species (at least among multicellular organisms) commonly makes both male and female gametes at the same time, or at different times, during its life – a condition known as *hermaphroditism*. Species in which an individual generates only one size of gamete are *dioecious*. In these species, one can classify whole individuals as either male or female, depending on the size of the gametes an individual produces. Sexual selection takes a whole-organism binary as the starting point and views hermaphroditism as a special case arising in peculiar circumstances. Social selection, on the other hand, takes hermaphroditism as the starting point and sees dioecy as a specialization for the ‘home delivery’ of sperm.

The theories of sexual selection and social selection each tells its own central narrative of male/female social dynamics.

*Universal sex roles.* According to sexual selection, males and females conform to near-universal templates: Darwin’s “passionate” male and “coy” female (or in today’s jargon, the “promiscuous” male and the “constrained” female). Though there are no general surveys of reproductive habits across all dioecious animal species, it is evident that these

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templates are, at best, unsubstantiated and, as generalizations, apparently false.

In insect species, for example, males are often as choosy as females. And in fish, surveys show that, of those species in which one or more parents care for the eggs, the male is more likely than the female to be the care provider. Birds often provide biparental care, whereas among mammals the female usually supplies the care.

It is hard, moreover, to distinguish 'care' from 'control.' Often, the parent who is caring for the eggs or young might actually be more concerned with the control of the young than in the provision of care for them.

No general pattern has actually been demonstrated about male/female sex roles throughout the animal kingdom, although the stereotypes that Darwin enunciated are widely accepted. Social selection believes that no necessary and universal sex roles exist; what each sex does is subject to negotiation in local circumstances. Any statistical regularity in sex roles may reflect a statistical frequency of circumstance, together with what constitutes a best bargain in such circumstances. Equally, if local ecology shows statistical regularities, so will the sex roles that emerge in those ecologies.

*Purpose of reproductive social behavior.*

The sexual-selection narrative explains what happens within a reproductive social system primarily in terms of 'mating.' Within a mating-based system, natural selection arises from differences in 'mating success,' and particular behaviors are understood by how they contribute to attaining plentiful mating opportunities. Females are regarded as a 'limiting resource' for males, and males compete for access to, and control of, mating opportunities with females.

In fact, evolution does not depend on mating as such but on the number of off-

spring successfully reared. Sexual selection elevates one component of reproduction, namely mating, into an end in itself. Meanwhile, social selection views reproductive social behavior as comprising an 'offspring-rearing system.' Within this system, natural selection arises from differences in the number of offspring successfully reared, and particular behaviors are understood by how they contribute to building, or maintaining, the social infrastructure within which offspring are reared. The principal male-female social dynamic is to determine bargains and to exchange side-payments that establish control over offspring and manage the offspring-rearing social infrastructure.

*Objective of female mate choice.* According to sexual selection, females select mates with the goal of endowing their own sons with the traits they find attractive in their mates. Females thus ensure that their own sons are destined to succeed in the mating game – a rationale called the 'sexy son hypothesis.' In fact, data are scanty that female choice is motivated more by indirect future genetic benefits than by direct present-day ecological benefits. In reality, females choose males who provide food and/or protection, rendering the importance of genes moot.

Under social selection, a female chooses mates based on maximizing the number of young she can successfully produce and rear – with help from her mates and from the social infrastructure. The criterion for female choice is an expectation of direct benefits from a male discounted by the probability that the male will renege on, or somehow be prevented from, delivering those benefits. Thus, a premium will be placed on the compatibility and health of the prospective partner. Health is important not as an indicator of 'good genes' but as a sign of com-

petency to deliver promised direct benefits.

*Male genetic quality.* According to sexual selection, males can be ranked in a hierarchy of genetic quality. In addition to the good genes that females are supposedly seeking in their mates, they aim to avoid bad genes. But if, generation after generation, female choice weeds out males with bad genes, then eventually no bad genes should remain, which presents an internal contradiction in the logic of sexual selection. Therefore, sexual selection is logically compelled to concoct genetic schemes, typically involving high mutation rates spanning polygenic loci, to replenish the supply of bad genes that are being continually eliminated by female choice. These additional schemes have never been tested much less verified.

Social selection, in contrast, states no hierarchy of genetic quality among males exists. If genes matter at all to female choice, females are choosing for genetic compatibility, and not overall genetic quality. All males are equivalent in genetic quality, excepting a rare fraction that obviously contain deleterious mutations and are present in a mutation-selection balance ( $1$  in  $10^6$ ).

*Bateman's principle.* In 1948, the English geneticist Angus Bateman published laboratory experiments with *Drosophila* that were presented as confirming Darwin's theory of sexual selection.<sup>6</sup> Bateman reported that a male's "fertility is seldom likely to be limited by sperm production but rather by the number of inseminations or the number of females available to him." Similarly, he claimed to have found in his flies an "undiscriminating eagerness in males and discriminating passivity in females" in accord with the

sexual-selection narrative. As a result, in sexual selection, male fitness has come to be defined primarily in terms of the number of matings, or 'mating success,' and female fitness in terms of egg production, or 'fecundity.' In this way, males and females are conventionally assumed to be governed by different definitions of evolutionary fitness.

The Bateman experiments are a cornerstone of sexual selection and have been widely cited in papers and textbooks. Over the last five years, however, many critiques have revisited the 1948 Bateman paper and found that Bateman overstated his results. Sexual-selection advocates have quoted selectively from what Bateman did report and have sometimes even attributed to Bateman quotations that they made up out of thin air. In social selection, Bateman's principle is nonexistent. Instead, both males and females share the same definition of fitness, namely, number of offspring successfully reared.

Social selection departs from sexual selection in the way it models behavior in reproductive systems. Sexual selection relies on competitive evolutionary game theory, considering particular behaviors as strategies. The prisoner's dilemma game is an oft-cited example in which the strategies of play are either to cooperate or to defect. The 'payoff matrix' tabulates the payoff to each player for all combinations of these strategies. The solution to the game is an evolutionary stable strategy (ESS): a combination of strategies for both players such that a mutant allele for some other combination cannot increase when rare.

This is a single-tier approach in the sense that particular behaviors are themselves viewed directly as evolutionary strategies. The problem is that it requires thinking of particular behaviors

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6 A. J. Bateman, "Intrasexual Selection in *Drosophila*," *Heredity* 2 (1948): 349–368.

as having a genetic basis, e.g., the gene ‘for’ cooperating, for defecting, for shyness, for aggressiveness, etc. Behaviors rarely have much direct genetic basis. But the single-tier approach forces narratives of genetic determinism.

Social selection approaches the modeling of social behavior as a two-tier problem: development on one tier, evolution on another. Particular behaviors develop as animals interact with one another, similar to how morphological structures develop through cell-cell contact during embryogenesis. A social system is a ‘behavioral tissue’: a system of phenotypes produced through interactive development.

In social selection, the developmental dynamics employ both cooperative and competitive game theory. Cooperative solutions mostly occur when parties play with coordinated tactics and with the perception of shared goals made possible through animal friendships. Even though a seemingly cooperative outcome may also result from competitive behavior, as in a standoff between weary combatants, the emphasis in social selection is on attaining cooperative outcomes through behavior that is explicitly cooperative, involving coordinated activities in pursuit of a shared goal. Social selection also envisions an evolutionary tier in which the payoff matrices and rules of play evolve based on traditional competitive evolutionary game theory. Particular social behaviors evolve indirectly as emergent properties from whatever payoff matrices and rules of play have themselves evolved. Thus, *evolution* produces the payoff matrix and rules of play, which then allow *development* to produce particular behaviors within the social infrastructure.

**S**ocial selection thus accounts for certain characteristics of sexual reproduc-

tion very differently from the way sexual selection views them.

*Parental investment.* According to sexual selection, the female has a higher parental investment than the male because the egg is bigger than the sperm. The sperm are considered ‘cheap’ and the egg expensive. This initial difference is then extrapolated to explain an entire suite of female and male behaviors, such as male promiscuity and female coyness.

Social selection, on the other hand, sees male and female parental investments as more or less the same initially. An ejaculate might typically contain  $10^6$  sperm while an egg is typically  $10^6$  times as large as a sperm. So the size of the ejaculate and egg are often about the same order of magnitude. Hence, male and female sex roles emerge not as a matter of logical necessity from gamete size, but from the local context.

*Sexual conflict.* The sexual-selection narrative regards a male and female as always fundamentally in conflict and male-female cooperation as a possible (and unlikely) secondary development. According to social selection, however, male and female mates begin with a cooperative relationship because they have committed themselves to a common ‘bank account’ of evolutionary success. Their offspring represent indivisible earnings. Hurting the other hurts oneself, and helping the other helps oneself, in terms of number of offspring successfully reared. As such, conflict develops only secondarily if a division of labor cannot be successfully negotiated.

*Male promiscuity.* According to sexual selection, males are naturally and universally promiscuous, reflecting the low parental investment of a sperm compared to an egg. In social selection, male promiscuity is a strategy of last resort that occurs when males are excluded from control of offspring rearing.

*Monogamy.* In sexual-selection theory, monogamy is a violation of the basic dictate that males should be promiscuous. Therefore, sexual selection explains away the instances of monogamous-pair bonds, including those of most birds and some mammals, as entrapment of males by females or as a default when no other mates are available.

Social selection distinguishes two distinct forms of monogamy: economic monogamy, an agreement to carry out the work of rearing offspring in teams of one male and one female, and genetic monogamy, an agreement not to mate outside the pair bond. Most monogamy is economic monogamy, and nothing requires economic monogamy and genetic monogamy to coincide. In social selection, economic monogamy emerges in ecological situations where the work of rearing offspring is most efficiently done in male-female teams rather than by solitary individuals or in teams of more than two individuals.

*Extrapair parentage.* Extrapair paternity (EPP) occurs when a male sires young in a nest other than the one he is working on with a female; extrapair maternity (EPM) occurs when a female deposits eggs in a nest other than the one she is working on with a male. Both EPPs and EPMs result in extrapair parentage. Sexual selection's primary literature describes extrapair parentage as 'cheating' on the pair bond: the male is said to be 'cuckolded'; offspring of extrapair parentage are said to be 'illegitimate'; and females who do not participate in extrapair copulations are said to be 'faithful.' This judgmental terminology reflects the failure to distinguish economic from genetic monogamy, and amounts to applying a contemporary definition of Western marriage to animals. Furthermore, EPPs are assumed to reflect the inevitable outcome of basic male pro-

miscuity, whereas EPMs are described as 'sexual parasitism.' Indeed, sexual selection refers to the females who deposit eggs in a neighbor's nest as 'brood parasites.'

For social selection, extrapair parentage is a system of genetic side-payments that stabilizes the social arrangement of economic monogamy when individuals differ asymmetrically in their capacities to contribute to rearing offspring. Distributed parentage also spreads the risk of nest mortality across a network of nests, acting as a social-insurance policy.

*Secondary sexual characteristics.* According to sexual selection, females choose mates on the basis of secondary sexual characteristics like the peacock's tail and the stag's antlers so that their own sons will be similarly attractive and successful at mating. The 'beauty' of a male's ornaments is how she apprehends his good genes; they are, in effect, 'condition indicators' of genetic quality.

Social selection sees ornaments, both male and female, differently: they are 'admission tickets' to power-holding cliques that control the resources for successful rearing of offspring, including the opportunity for mating, safety of the young from predation risk, and access of the young to food. Accordingly, a peacock's tail, a rooster's comb, etc., facilitate male-male interactions, and females are indifferent to them.

Admission tickets are expensive because the advantages to membership in a clique reside in the power of monopoly, which is diluted when membership is expanded. By requiring a high price of admission, the monopolistic coalition is kept exclusive, maximizing the benefits to those within. Ornamental admission tickets belong to a class of traits called 'social-inclusionary traits' that are needed to participate in the social infrastruc-

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ture within which offspring are reared. Other traits include those needed for communication and cognition within the social infrastructure. Not possessing such traits, or not participating in social-inclusionary behaviors, is reproductively lethal.

The strong natural selection imposed by the requirement of membership in power-holding cliques can produce the very fast evolution, including possibly runaway evolution, that has long been the signature of sexual selection. Admission tickets are not the only way to enter power-holding cliques, however. Conceivably, individuals might be recruited to join, and the admission ticket waived, if they supply capabilities or assets valued by the other members. But if the sole benefit from membership is monopolistic, then membership should require an expensive ticket.

Two phenomena in particular present challenges to sexual selection.

*Sexual monomorphism.* Species in which males and females are identical in appearance pose a direct contraction to Darwinian templates, which say males should be showy and females drab. Darwin dismissed these species as having females that lack an aesthetic sense. In social-selection theory, sexual monomorphism reflects the absence of same-sex power-holding cliques whose membership requires admission tickets. This should occur in ecological situations where the most economically efficient coalition is the coalition of the whole.

*Sex-role reversal.* Species in which the male is drab and the female showy, the reverse of the peacock/peahen comparison, also contradict the Darwinian 'norm.' In sex-role-reversed species, the male provides more parental investment than the female does by carrying and/or tending the eggs – so the males are

in short supply for mating relative to females. In this situation, sexual selection claims that females compete with one another for access to males and become the showy sex, whereas the male remains drab, thus reversing the putative peacock story. This account, even if it were true, cannot be an *explanation* of sex-role reversal – it is merely a *redescription* of the phenomenon. Sexual selection does not say why the male in these species should happen to be the sex providing the higher parental investment. Moreover, the mere existence of sex-role-reversed species challenges a basic tenet of sexual selection – that sex roles can be traced to gamete size – because sex-role-reversed males, like all other males, produce tiny sperm. Thus, gamete size does not entail sex role.

Reversed sex roles are not especially problematic for social selection, because sex roles are always negotiated in local ecological situations anyway. It is in a male's interest to secure some control of the eggs, thereby retaining some control of his evolutionary destiny. In some ecological circumstances, doing so may mean the male winds up with more parental responsibility than the female does.

Social selection provides peripheral narratives for diversity in gender expression and sexuality.

*Gender multiplicity.* Many species have more than one type of male and female, so that comparing the males to just one template and the females to another is impossible. I call each such template a 'gender.' In many species of fish, lizards, and birds, for example, one male gender has a large body size at reproductive age but must survive several years to attain that size, thereby suffering a high cumulative risk of mortality. But once large, such a male can command a territory

and defend eggs laid in it. Another gender of males reaches reproductive age sooner, does not defend territories, and fertilizes eggs that are in the territories defended by large males. These species exhibit two male and one female genders.

A three-male pattern is observed in some fish and birds, where the large male solicits the help of a medium-sized male. The pair together maintains the territory and participates jointly in courtship with females. The large male allows the medium male to fertilize some of the eggs in the territory. A third type – the small male – meanwhile remains as a competitor to the large- and medium-sized males, fertilizing some of their eggs in spite of their attempts to chase him away.

These species with multiple male and female genders all defy any attempt to apply sexual-selection theory directly because that theory posits only one template each for male and for female appearance and behavior. As a result, sexual selection theory has been augmented with additional narratives to account for more than one gender per sex.

The problem with sexual selection, though, is that it takes the large territory-holding male gender as the reference male, while considering the other genders of males as ‘alternative mating strategies’ and defining them as ‘sexual parasites.’ A pejorative language masquerades as description throughout these peripheral narratives of sexual selection. Sexual selection terms the small non-territory-holding male a ‘sneaker’ who ‘steals’ copulations that rightfully belong to the territory-holding male. It depicts the sneaker as stealthily entering the large male’s territory through a back door.

In fact, small males are often more numerous than large males, so the small

male typifies ‘maleness’ in the species more than the large male does; and the small males often band together in the open to chase away the large male and fertilize eggs in the territory, rather than entering singly and stealthily.

Social selection, in contrast, extends economic theory for the elemental one-male-one-female economic team to larger teams with more ‘social niches.’ A reproductive social group subsumes the concept of a ‘family,’ which is a reproductive social group whose members happen to be genetically related. In a reproductive social group, some members are ‘prezygotic helpers’ – animals that assist in bringing about courtship and mating – together with ‘postzygotic helpers’ – members who remain at the nest to help rear the offspring that have already been born. Those not included in the reproductive social group’s coalition form other arrangements to oppose it, either singly or in coalitions of their own.

In this conceptualization, coalitions may form containing medium-sized males who assist in recruiting females to the nests of the large males who control eggs by means of controlling territory. A large-male/medium-male coalition may then be opposed by a small-male coalition that competes to control the eggs. The complex social dynamics for these scenarios can be approached with cooperative game theory, which deals with the formation and dissolution of coalitions and with the distribution of the team’s payoff among its members.

*Feminine males.* In species with multiple male genders, one gender often has colors or markings somewhat resembling those of females. In popular writing, I have termed these males ‘feminine males.’ In sexual selection, feminine males are called ‘female mimics’ – sexual parasites who steal the reproductive

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investment of territory-holding males through deceit. A female mimic is disguised as a female to fool the territory-holding male into allowing him to enter the territory-holding male's harem and mate with his females.

This story has not been demonstrated. The capacity of a feminine male to fool a territory-holding male into 'thinking' it is a female implausibly requires gullibility by the territory-holding male as well as craftiness by the feminine male. In fact, the territory-holding male is often a visual predator with well-honed skills at sizing up and identifying prey from a distance; he is not likely to be fooled by a feminine male who only imperfectly resembles a female. Instead, the courtship between the territory-holding male and the feminine male is perhaps best thought of as a job interview prior to joining the team, rather than an elaborate deception.

According to social selection, markings and colors on animals represent 'body English' – how animals tell one another what their social role is, what their intentions are, and what activities they promise to perform. Feminine males are simply participating in a conversation on topics and with words used more frequently by females than by masculine males.

*Masculine females.* In sexual selection, masculine females are discussed under the rubric of 'female ornaments' – hanging skin flaps (wattles), colored patches of feathers, antlers, and so forth – usually considered male ornaments. Darwin dismissed out-of-place ornaments as male traits accidentally expressed in females – a developmental error. According to social selection, however, masculine females are simply the reverse of feminine males, namely, a female using body English to converse on topics and with words used more frequently by

males than by feminine females. Such conversations might involve establishing and defending territories in species where these tasks are sometimes carried out by females. Masculine females appear underreported because feminine males draw more sensational attention.

*Homosexuality.* Biologists are just now starting to appreciate the extent of homosexuality as a natural part of the social systems of animals in their native habitats. Homosexual behavior is now documented in the primary literature for over three hundred species of vertebrates, not to mention invertebrates; and many cases are reported in news media, popular magazines, and wildlife, agricultural, or hobbyist sources. In some species, homosexuality is mostly between males; in others, mostly between females; and in still others, both. In some, homosexuality is relatively uncommon, occurring in about 10 percent of matings; and in others it is as common as heterosexual matings, accounting for 50 percent of all matings.

Sexual selection explains homosexuality as an inadvertent mistake, as deceit, or as a deleterious trait maintained through peculiar population-genetic mechanisms that promote the persistence of bad genes. A typical deceit narrative postulates that a small male sneaks into the territory of a large male, tires the large male by acquiescing to homosexual copulation, and then proceeds to mate with the females in the large male's harem. This behavioral narrative credits homosexual behavior as adaptive to the small participant, but views it as exploitation – the gay animal exploits the straight animal.

Meanwhile, population-genetic narratives of homosexuality consistently portray homosexuality as a genetic defect or a maladaptive disease maintained by peculiar genetic schemes, such as sexual-

ly antagonistic selection, in which the genes that cause homosexuality decrease fitness in one sex but are maintained in the population because they increase fitness in the other sex. These approaches attempt to encode a homophobic narrative of homosexuality as deleterious and pathological into the hypothesis structure of evolutionary biology, and uncritically ignore the many alternative adaptive hypotheses for homosexuality in the behavioral literature.

According to social selection, not only is homosexuality natural and adaptive, but its explanatory narrative focuses on positive contributions to both parties. Homosexuality is grouped with many other social behaviors involving physical intimacy, such as mutual grooming, mutual preening, sleeping together, rubbing tongues together, and even making interlocking calls and other vocalizations. These behaviors allow two animals to work together as a team, to coordinate their actions so they make moves simultaneously. Furthermore, these behaviors allow animals a tactile sense of each other's welfare. Since, in social selection, the outcomes of cooperative game theory are realized through team play and perception of team welfare, homosexuality is one of the physically intimate behaviors between animals that enable team play.

**H**ow might one apply these contrasting theories to the human case?

*Human attractiveness.* If the theory of sexual selection applies to humans, women are supposed to find handsome men who display traits indicating their genetic quality. Conversely, men are supposed to be promiscuous. According to social selection, males and females choose each other equally, with the criterion for both being compatibility of circumstance, temperament, and incli-

nation that underlies effectiveness at raising offspring in the context of a human social infrastructure.

*Human brain.* Sexual selection posits the human brain as a counterpart of the peacock's tail, an ornament used by men to attract women. One imagines a man using his big brain to compose lovely sonnets to woo his mate. The problem then is to explain why women have brains. Is a woman's brain a 'female ornament,' as out of place in a woman as a gaudy tail on a peahen? Sexual selection postulates that females use their brains to appreciate the brains of males – only big-brained women are turned on by the sonnets of big-brained men. Social selection, on the other hand, views the human brain as a social-inclusionary trait, a trait needed to participate in the social infrastructure within which offspring are reared. This trait is equally necessary in both men and women because both share the work of rearing offspring.

**O**ne might have anticipated that evolutionary biologists would react with glee to an alternative theory to sexual selection. After all, challenges to the theory of relativity, or to the theoretical basis of gravity, elicit calls on Congress to fund expensive experimental facilities lest billiard balls suddenly change trajectories or gravity suddenly evaporate. If sexual selection is wrong, then surely we need to get the matter right lest sex itself disappear. This threat to our personal security seems grave enough to usher in a bonanza of funding so that evolutionary biology might champion the noble mission of making the world safe for sex.

But no, rather than seizing the research opportunity that an alternative to sexual selection provides, evolutionary biologists have, for the most

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part, tried to discredit me personally as biased. Even before my book *Evolution's Rainbow* was published, the editorial staff of *Nature* in 2003 encouraged a young journalist, Virginia Gewin, to write: "Some scientists privately wonder if – whether she likes to admit it or not – Roughgarden's own experiences of social exclusion have biased her view of the natural world."<sup>7</sup> When the book appeared in 2004, Alison Jolly's review in *Science* identified me as a "transsexual professor" in the second sentence.<sup>8</sup> Then Sarah Hrdy's review in *Nature* continued with, "This evolutionary biologist becomes a woman, and only then do the problems occur to her."<sup>9</sup> A month later, Robin Dunbar ridiculed my book in *Trends in Ecology and Evolution* (TREE): "Readers of TREE will no doubt be pleased to know that sexual selection is dead so they can now get on with research into more useful topics."<sup>10</sup> Dunbar concludes with the admonition, "It is almost impossible to retain a sense of dispassionate objectivity when you see yourself as an object of your own research." Dunbar is happily unaware that this applies to him as well.

Jerry Coyne followed up in the *Times Literary Supplement*. After outing my former name in the second sentence of his review, he charges that my "laundry list is biased. She ignores the much larger number of species that do conform to sexual selection theory, focusing entire-

ly on the exceptions." In fact, no one knows how many species conform to Darwinian sex-role templates, and many thousands do not, as I have already discussed. Coyne accuses me of being anthropomorphic but then goes on himself to illustrate sexual-selection theory with a human example: "The Guinness Book of Records awards the laurels for reproductive output to a Moroccan emperor who sired more than 900 offspring. The female record – though in some ways more remarkable – is a mere sixty-nine."

Michael Ruse, a philosopher who has written books advocating Darwinism, continued in the *Toronto Globe and Mail*. He dismisses *Evolution's Rainbow* as a "cryptic autobiography" and "polemic" against sexual-selection theory directed to campus audiences in "areas like cultural studies that are big into . . . the hegemony of heterosexism and all that sort of thing."<sup>11</sup> Ruse also plays the transsexual card, excusing himself by saying, "Normally, one would not start discussing a person's thesis by talking about the person herself, but in this case it is both legitimate and necessary." He goes on to argue that the concept of gender cannot be widened to include animals because a bullfrog could never say, "I was a man trapped in a woman's body." Ruse objects to theorizing that homosexuality in animals evolved to promote bonds because this cannot explain human "bathhouse culture."

The gold medal for insult goes to a Peter Conrad writing in a U.K. Sunday newspaper, *The Observer*, *Guardian Unlimited*. He declares *Evolution's Rainbow* to be a "practical joke," refers to San Francisco as "frisky," and disparages my "strange allegorical surname" by

7 V. Gewin, "Joan Roughgarden Profile: A Plea for Diversity," *Nature* 422 (2003): 368–369.

8 A. Jolly, "The Wide Spectrum of Sex and Gender," *Science* 304 (2004): 965–966.

9 S. Hrdy, "Sexual Diversity and the Gender Agenda," *Nature* 429 (2004): 19–21.

10 R. Dunbar, "Is Sexual Selection Dead?" *Trends in Ecology and Evolution* 19 (2004): 289–290.

11 M. Ruse, "Why Not a Third Sex? And a Fourth, and . . ." *Toronto Globe and Mail*, July 10, 2004.

claiming my life consists of “tending her mutated physique as if it were a rough garden that has now been weeded and manicured into femininity.”<sup>12</sup>

Another angry defense of sexual selection was broadcast by Michael Ghiselin in the magazine *California Wild*. Ghiselin claims a previous article of mine in the same magazine “gives no indication of the author’s ulterior motivations for writing it.”<sup>13</sup> He proceeds to out me as someone who “at age 51 . . . had himself transformed into Joan Roughgarden” and dismisses *Evolution’s Rainbow* as “a work of self-justification.” Meanwhile, Ghiselin privileges himself as an “honest seeker after truth” who does not “want to see the issues misrepresented.”

Similarly, together with collaborators, I recently presented in *Science* our two-tier alternative to sexual-selection theory, introducing cooperative game theory for the behavioral tier, as well as conventional competitive game theory for the evolutionary tier.<sup>14</sup> It evoked ten indignant letters of reply that were also published in *Science*, representing over forty authors.<sup>15</sup> Nick Atkinson of *The Scientist* contacted the sexual-selection defenders and recorded comments ranging from “the ‘new’ theory is merely part of the existing body of Darwinian sexual selec-

tion theory,” from Kate Lessells of the Netherlands Institute of Ecology, and “sexual selection theory . . . happily includes all of the points Roughgarden et al. try and make,” from David Shuker at the University of Edinburgh, to “many people felt that this was completely shoddy science and poor scholarship, all motivated by a personal agenda,” from Troy Day at Queens University in Canada.<sup>16</sup> Put together, these comments claim at once that social selection is part of sexual selection and also bad scholarship, a position sexual selectionists should find discomforting.

Sexual selectionists also attempt to intimidate by noting I have been the “target” of critiques “involving more than 50 distinguished behavioral ecologists,” according to a recent anonymous grant reviewer, as though I should now be silent. The panel summary then charges that “the PI [Roughgarden] does a major disservice to the field and to her own research . . . . The panel feels that the PI is setting up a straw man.” Is sexual selection a straw man?

In response to this devastating reception, I sought to change my name and escape to Tierra del Fuego. But the village elders there declined my visa application. Having now been declared *persona non grata* even to the ends of the earth, I am left no choice but to stand my ground. Darwin’s theory of sexual selection is locker-room bravado projected onto animals and then retrieved as though a fact of nature.

Fortunately, the relentless dirge of anger directed against *Evolution’s Rainbow* was punctuated briefly in 2005, when the book received thoughtful and extensive reviews by Robert Dorit in *The*

12 P. Conrad, “Frisky in Frisco,” *The Observer, Guardian Unlimited*, August 1, 2004.

13 J. Roughgarden, “The Myth of Sexual Selection,” *California Wild* (Summer 2005); M. Ghiselin, “Sexual Selection,” *California Wild* (Winter 2005).

14 J. Roughgarden, M. Oishi, and E. Akçay, “Reproductive Social Behavior: Cooperative Games to Replace Sexual Selection,” *Science* 311 (2006): 965–969.

15 Etta Kavanagh, ed., “Debating Sexual Selection and Mating Strategies,” *Science* 312 (2006): 689–697.

16 Nick Atkinson, “Sexual Selection Alternative Slammed: Biologists Write to *Science* to Defend the Theory of Sexual Selection,” *The Scientist*, May 5, 2006.

*American Scientist* and Douglas Futuyma in *Evolution*.<sup>17</sup>

The criticisms of *Evolution's Rainbow* and later work do not deal with substantive issues, and instead employ personal attack to deflect attention from the seriousness of sexual selection's limitations. I have evidently stumbled upon a Darwiniate. The invective in the criticisms may signal unease at unraveling a cover-up, a fear that decades of professional and personal investment in the sexual-selection narratives will collapse.

The invective may also scratch the vein of a deep-seated transphobia among evolutionary biologists. Legitimizing diverse expressions of gender and sexuality is clearly threatening. Ghiselin issues the threat explicitly:

Had Roughgarden simply argued that there is more to reproductive strategies than just male combat and female choice, and presented some reinterpretations of the data, there would have been no reason to respond. But here we have an effort to discredit perfectly good science.

Thus, it would be okay to add a little fluff to sexual selection to account for gay and gender-bending animals, so long as I do not touch the central narrative.

I invite readers to consider the possibility that sexual selection is completely wrong because it started out on the wrong track, and that refusing to reconsider sexual selection's grounding assumptions is leading subsequent research to compound the original errors. Only by devising and testing alternative evolutionary theories of reproductive social behavior can we truly strengthen evolutionary biology.

17 R. Dorit, "Rethinking Sex," *American Scientist* 92 (5) (September – October 2004); D. Futuyma, "Celebrating Diversity in Sexuality and Gender," *Evolution* 59 (2005): 1156 – 1159.