



Challenging Darwin's Theory of Sexual Selection

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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.

Social selection thus accounts for certain characteristics of sexual reproduc-

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-

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

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.

How 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.