Making Males Aggressive and Females Coy: Gender across the Animal-Human Boundary

exual selection, as conceived by Charles Darwin in the mid-nineteenth century, explained the origins of phenomena in the animal kingdom that could not be attributed to natural selection—why males and females differed in their appearance and behavior and the presence of beauty.¹ To explain beauty in the natural world—from the gregarious displays of wild turkeys in the spring to the vibrant contrast of red cardinals against the winter snow—without reference to our own pleasure presented a difficult problem for biologists committed to naturalistic explanations. Darwin suggested mate choice as a solution: beauty was useful for animals because it helped them attract mates. The idea of choice vexed other zoologists, however, because it seemed to grant to animals the same capacity for aesthetic appreciation and decision making that humans enjoyed.

As Donna Haraway's *Primate Visions* (1989) so vividly illustrates, the relationship between the animal and the human informs our scientific and cultural perceptions of what it means to be male or female today, much as it did for Darwin. In this article, I interweave two polarities, animal and human, male and female, to elucidate the evolution of biological constructions of animality and gender. In the early decades of the twentieth century, few biologists found Darwin's proposed mechanism for sexual selection—female choice—plausible, as they rejected the idea that animals possessed the capacity to aesthetically evaluate and choose a mate. Animals in the early twentieth century functioned as mechanical foils against which zoologists sought to define what it is to be human. After

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¹ Darwin first introduced sexual selection, including both competition between males and selection by females, in *On the Origin of Species* (1859, 87–89, 156–58, 196–99), and he extensively elaborated sexual selection in *The Descent of Man, and Selection in Relation* to Sex (1871).

[Signs: Journal of Women in Culture and Society 2012, vol. 37, no. 4] © 2012 by The University of Chicago. All rights reserved. 0097-9740/2012/3704-0010\$10.00 World War II, however, animals as social beings became sources for understanding our human instincts. Men were quickly bestialized because of their association with aggressive, warlike behavior, whereas women were exempted from such degenerate stereotypes. Yet, less than a decade later, biological anthropologists and zoologists began to frame female animals as possessing equal agency, albeit by acting sexually coy and exercising their natural prerogative—female mate choice. A history that combines theories of animal and human behavior thus provides a dynamic tool for thinking about the scientific construction of sexual roles throughout the century.

Feminist scientists and historians have incisively explored the gendered dimensions of Darwin's theory of sexual selection.² Darwin proposed two mechanisms by which sexual selection might function. The first, female choice, took place when males displayed their finery and females compared the males, selecting one with whom to mate. The second, male-male competition, occurred when males fought over access to females and resulted in the development of armor, horns, antlers, or other weapons of minor destruction. The result of sexual selection over time was twofold: the traits selected helped animals obtain mates and leave more offspring (rather than fit their environment, as expected with natural selection), and males and females began to look and act differently—females became coy and males ardent.

Although "coy" as a term applied to the mating behavior of female birds and women has a long tradition (e.g., see "Tuesday" 1756, 162), in zoological circles coy females came to be primarily associated with Darwinian sexual selection and Darwin's description of females as requiring courtship to overcome their natural tendency to run from males (Darwin 1871, 1:273). Darwin seems to imply that despite their apparent passivity, by differentially fleeing suitors females were choosing either the least distasteful or most attractive male with whom to mate. Darwin's rival discoverer of natural selection, Alfred Russel Wallace, also used the term in debates over female mating behavior (Wallace 1871, 178). Following their example, agronomist Angus John Bateman described the reproductive behavior of female fruit flies as passive (Bateman 1948, 350). In turn, citations of Bateman's work on the "traditional coyness of the female" appeared again among evolutionary biologists in the late 1960s (Williams 1966, 183; see also Trivers 1972). By the mid-1970s, these evolutionary accounts of coy females were gaining wider readership among a popular academic audience (Wilson 1975; Dawkins [1976] 2006). Yet not all zoologists meant the same thing when they used the word "coy." For Darwin and Wallace, for example, being sexually coy was a passive quality; it was a biological consequence of being female (Darwin 1871, 1:273; Wallace 1871, 178). For evolutionary biologists Robert Trivers and George Williams, on the other hand, females actively played coy as part of an evolutionary strategy to evaluate the potential commitment of the male to participating in offspring care (Williams 1966, 186; Trivers 1972, 148–49). This difference between biological identity and reproductive strategy underpinned two rather different ways of looking at animal behavior as the result of instinct or negotiation.

The standard history of sexual selection—and by association, female choice—frames these works in a single linear heritage, carrying Victorian stereotypes of "eager" males and "comparatively passive" females into the 1970s (Darwin 1871, 1:273). It is a story of mostly male biologists who either (in a sympathetic reading) botched the transition from their favorite model organism to primate behavior or (less sympathetically) imposed their own biases about sex and gender onto their animal subjects.³ Either way, for many feminist critics of evolutionary accounts of human behavior, zoologists' conclusions became suspect for naturalizing a vision of women as behaviorally passive, sexually coy, and inevitably maternal.⁴ This was so much the case that biologists like Sarah Blaffer Hrdy and Patricia Gowaty, who identify as both feminists and evolutionary theorists, have felt the need to justify their evolutionary research as feminist (Hrdy 1999a, xiii–xxxii; Gowaty 2003).

In this article, I add another dimension to this history: the relation between animal and human minds. On both sides of the Atlantic, theories of animal minds in the early twentieth century—including both American behaviorism, which focused on the capacity of conditioning to alter the behavior of an animal or person (Watson 1914; Skinner 1938; Lemov 2005), and European ethology, which focused instead on the evolution of behavior in natural environments—tended to frame animal behavior in

² Biologists' critiques of "coy" as a descriptor of female mating behavior have taken at least two forms: male and female parental investment may not be so different after all; and, even if females do invest more in their offspring, that does not make them passive. For example, see Hrdy (1986), Tavris (1992), Gowaty (1994), Tang-Martinez (2000), and, most recently, Roughgarden (2009). For historical and philosophical critiques of coy females, see, e.g., Bleier (1984), Haraway (1989), Russett (1989), Hubbard (1990), and Cronin (1991).

³ See Bleier (1978), Hrdy (1986), Cronin (1991), and Tavris (1992).

⁴ See, e.g., Tanner (1981), Zihlman (1985), Fedigan (1986), Haraway (1989), Cronin (1991), and Gowaty (2003).

mechanistic, reactive terms.⁵ Biologists from both traditions emphasized a fundamental gulf separating human and animal minds. Humans could manufacture and use tools to manipulate their environment, communicate abstract concepts through language, and choose rationally—animals could not. Thus, for much of the century following Darwin's publication of *The Descent of Man, and Selection in Relation to Sex* (1871), biologists were largely unwilling to grant animal minds the cognitive capacity of choice that Darwin's theory seemed to require.

By the 1960s, however, biologists and anthropologists increasingly described animals as active agents due to their concern with the seemingly innate tendency of men to wreak war and violence in society. The popethology and pop-anthropology literature of the 1960s emphasized the importance of atavistic animal instincts in humans as a possible cause of male aggression (Ardrey 1961; Lorenz 1966). Men lacked appropriate outlets for their natural aggression, and even in combat the ability to kill at great distances prevented one-on-one physical encounters that might diffuse soldiers' aggressive drives. Simultaneously, American and British biological anthropologists took advantage of the newly decolonized African savanna to study other social primates.⁶ Baboons were seen as the prime representative of a primate species in an ecological transition from trees to savanna, much like human ancestors had been millions of years earlier (DeVore 1965). Primatologists saw parallels between the importance of male aggression in structuring baboon social interactions and the issue of aggression in humans. In equally gendered stereotypes, primatologists and evolutionary theorists saw women and female primates as less likely to succumb to the ravages of anger or the aggressive instincts that beset men or male baboons. In other words, through a newfound concern with the instinctual aggression of men following the Second World War, male animals were rehabilitated within theories of animal behavior into active, plotting, hunting, and social beings. This new vision of animals as capable of manipulating their social environments began to collapse the hard and fast division between human and animal minds that had largely dominated the study of animal behavior in the first half of the twentieth century.

⁵ See von Uexküll ([1909] 1957), Tinbergen (1951), Lorenz (1952), and Burkhardt (2005).

⁶ The strong tradition of primatology in Japan developed under a different set of cultural circumstances and is beyond the scope of this article (see Asquith 2000; de Waal 2003). It is worth noting, however, that these studies focused on both female and male roles as actively contributing to the social structure of Japanese macaques (see, e.g., Imanishi and Altmann 1965).

The minds of female animals were rehabilitated secondarily within this framework, through the recognition that female choice in animals could actively alter male behavior and, in humans, that women's work contributed substantially to the internal social dynamics and long-term survival of the group. Biologists and anthropologists appropriated sexual selection and female choice as active evolutionary strategies only after animal minds were considered capable of true choice. Additionally, even playing coy represented only one possible mating strategy females might adopt. As biologists came to know more about female social interactions, any adherence to a strict promiscuous-male/coy-female framework came under attack from within the scientific community.

In short, during the first half of the century, scientific attempts to use choice as a biological characteristic distinguishing humans from other animals yielded theories of animal behavior that emphasized the unconscious nature of animal actions. Biologists discounted Darwinian female choice not because it involved females but because the theory required that animals possess the mental capacity to choose a mate. During the second half of the century, biologists and anthropologists began to investigate social interactions in primates and other animals as models of early human societies. As scientists recognized that humans were more animal-like than they had thought, animals reciprocally became capable of being more human—more active, more competitive, more coy—than in earlier decades. Biologists made females coy as a result of making males aggressive, and both moves required rethinking a fixed boundary between animals and humans.

Negotiating choice: Animal minds and human instincts

In the decades following Darwin's publication of *The Descent of Man, and Selection in Relation to Sex* (1871), most biologists believed that humans differed fundamentally from animals, whether because humans possessed a soul whereas animals did not or because humans, through the development of conscious thought and civilization, were no longer governed by the same natural forces that dictated animal survival and reproduction. Turn-of-the-century concerns over the increasing remove of human civilization from nature inspired both conservation movements, to preserve what little wilderness remained, and eugenics movements, to protect the future of Western civilization now that natural selection was no longer at work in human society (Richardson 2003; Kingsland 2005). In studies of animal behavior, similar concerns led biologists to frame the actions of animals as the result of either behavioral or evolutionary programming. Such mechanical frameworks worked well for understanding how animals learned to solve puzzles or react to a threat from another individual but not for explaining why some species were far more beautiful than others. The eye-catching plumage of many male birds posed a particular problem for evolutionary biologists because they surmised that if the brightly colored feathers caught their attention, then surely it would also attract the attention of animal predators (Kellogg 1907). By following the thread of Darwin's theory of female choice as applied to birds, we can trace changing assumptions about the animal mind throughout the first half of the twentieth century.

Darwin's theory of natural selection, based on competition among members of the same species for limited ecological resources, was a powerful tool that he used to explain the speciation of plants and animals and how they became adapted to the environments in which they lived (Darwin 1859). Yet Darwin despaired of using natural selection to explain beauty in animals because the extravagant traits so lauded by humans hardly seemed to help the animals that exhibited them survive in their local environments. If anything, the traits made the animals more visible to predators and made it harder for them to escape. Additionally, he could not see how natural selection might explain why males and females differed in their appearance and behavior. Surely any trait that helped a male rabbit escape a fox would also help a female rabbit! Sexual selection provided an answer, which Darwin applied to animals and humans equally. In humans, he suggested, sexual selection might explain the origin of races (Desmond and Moore 2009), which he saw as providing a similar problem to that of sex differences: both were stable variations in the appearance of groups of individuals within a single species. I mention this by way of illustrating that for Darwin animal and human minds were distinguished by differences in degree, not in kind (Richards 1987). For example, in The Descent of Man, and Selection in Relation to Sex, Darwin argued that just as a human breeder could "give elegant carriage and beauty to his bantams, ... female birds, by selecting ... the most melodious or beautiful males, according to their own standard of beauty, might produce a marked effect" (Darwin 1859, 89). Like people, animals could compare and evaluate the aesthetic beauty of other individuals.

Many of Darwin's contemporaries, including Wallace, found his failure to categorically distinguish between animal and human minds problematic at best. Framed within his increasingly spiritualist understanding of life, Wallace argued instead for a strong divide between human and animal mental capacities. Whereas animals were subject to natural selection as a mechanism for environmental adaptation, human capacity for mental deliberation allowed us to escape its ravages. Wallace insisted that animals could not choose and therefore sexual selection was not at work in birds, even though mate selection could be a powerful force of evolution in human society. In his book *The Social Environment and Moral Progress*, Wallace wrote that "sexual selection possesses the potentiality of acting in the future so as to ensure intellectual and moral progress, and thus elevate the race to whatever degree of civilization and well-being it is capable of reaching in earth-life" (1913, 140–41).

Wallace provided his own explanation of sex differences in the coloration of birds based instead on natural selection. He contended that beautiful male plumage was a physiological result of the body's exuberance. Patches of brightly colored feathers would be produced wherever excess energy was expended, resulting in the red chest of the singing robin, for example, or the male peacock's blue train, which he delighted in shaking before the female. Wallace reasoned that males were generally more active than females, so logically we should expect that males would also be more colorful than females. The real phenomenon in need of explanation, he continued, was why the plumage of females was so consistently nondescript and brown. This Wallace easily explained as the result of natural selection for camouflage during the nesting season. If a female were caught by a predator, then she would lose her own life and the future lives of her offspring. For Wallace, then, the differences between male and female coloration were the result of natural selection for female maternal success, not sexual selection for male grandeur (Wallace 1877).

For mathematical geneticist Ronald Fisher, much as for Wallace, natural selection could explain the evolution of the organization and physical structures of animal and human bodies. He reserved the evolution of human ethics, aesthetics, and morality as the special jurisdiction of sexual selection: "All the refinements of beauty, all the delicacy of our sense of beauty, our moral instincts of obedience and compassion, pity or indignation, our moments of religious awe, or mystical penetration" were the result of conscious selection in humans (Fisher 1914, 309). Marriage selection, a form of mate choice in humans, formed a crucial part of positive eugenic discourse throughout the first decades of the twentieth century (Richardson 2003).⁷ This association of choice and aesthetic

⁷ Literature that focused specifically on mate choice in animals was less common, resulting in a spottier chronology. For a more complete history of sexual selection during this time, see Milam (2010).

beauty lay at the heart of Fisher's conviction that sexual selection was more important for the improvement of humanity's biological future than it was for animal evolution.

To explain the evolution of beauty in animals, who lacked the higher consciousness of humans, Fisher (1930) proposed a theory called "runaway" (137) sexual selection. In runaway sexual selection, female choice for a trait and the male expression of that trait became genetically linked and so coevolved together. If a female, for no particular cause, happened to prefer the male with the longest tail, then their offspring would consist of males with long tails and females who preferred long-tailed males. Over several generations, Fisher posited, the average tail length of the males would increase and female preference for long-tailed males would grow stronger. To be the longest-tailed male of the group, a male's tail would have to be longer than his father's or his grandfather's before him. Even if males with extraordinarily long and bright tails caught the eyes of predators, selection for this trait would continue as long as the males possessing the trait managed (on average) to leave more offspring than those males with duller or shorter tails. Through female choice, then, evolution could drive populations to express traits that decreased individuals' chances of survival (Fisher 1930, 131-39).

Despite his use of bird plumage in describing the effects of runaway sexual selection, it seems likely that Fisher still had human evolution in mind. For example, he used the runaway process to explain male heroism in battle (Fisher 1930, 162, 247). As with bird plumage, he found it difficult to explain altruistic tendencies solely in terms of natural selection, which he thought should act to cull such phenomena from a population very quickly. He hoped that human mate choice for good, moral characters would help the British population recover from their huge losses of promising young men in World War I. Yet mate choice gone wrong could be devastating. He worried that the evolutionary future of Britain was in grave danger because men and women of the working classes were apparently reproducing at a higher rate than their more genteel countrymen. Fisher devoted the second half of The Genetical Theory of Natural Selection (1930) to describing the evolutionary causes of contemporary social degeneration and outlining a plan of economic incentives designed to alleviate the difference between the birth rates with which he was so preoccupied. Although Fisher used mate choice as a tool to describe the evolutionary past and future of human society, he doubted the ability of any biologist to demonstrate the efficacy of female choice in animals.

Another biologist writing in the late 1930s who deemed it unlikely that animals could choose their mates was zoologist Julian Huxley. Huxley

argued that apparent female choice in animals was really the result of some males courting more vigorously than others and that most sex differences in appearance and behavior could be attributed to the need for sex recognition, aggression toward potential competitors, and warnings to predators (Huxley 1938). To him, all these factors were really natural selection. not sexual selection. Based on earlier observations of the courtship behavior of the great crested grebe, Huxley noted that most courtship displays took place after pairing. Courtship was thus key to extended pair bonding, not to the initial choice of mates. Huxley drew a bright line between human and animal cognitive abilities. A popular textbook that Huxley coauthored proposed that "the human lover woos with the cerebral cortex, he (or she) is plastic and responsive, and adapts the means to the occasion." In stark opposition, "the impassioned bird woos ardently but automatically with the corpus striatum. . . . The human lover may do a thousand things; the courting bird is an elegant determinate machine" (Wells, Huxley, and Wells 1931, 742). By describing animal behavior as automatic and determinate, Huxley hoped to professionalize the study of animal behavior and distance the growing field from the anthropomorphic stories he associated with amateur writings (Burkhardt 2005).

Huxley also worked with a group of biologists seeking to make zoology more evolutionary in focus. The research of population geneticists like Theodosius Dobzhansky and zoologists like Ernst Mayr had transformed definitions of female choice from a matter of beauty or aesthetic comparison to one of recognizing a mate of the appropriate species.⁸ Rather than observing the mating behavior of a few individuals, evolutionary biologists turned to statistical analyses of many copulations. If only a male of the right species could stimulate a female to mate, then biologists could tell if two populations were really separate species by allowing them the opportunity to interbreed. If just a few individuals did, say less than 1 percent, then the populations were reproductively isolated-they were "good" species. If a much higher percentage of individuals interbred, perhaps 30 percent, then the two populations were simply subspecies. Population geneticists began to use female choice as a diagnostic tool to analyze the process of speciation rather than looking at mating behavior as a mechanism for changing the appearance of a single species.

Although most animals could fit within this new evolutionary agenda, there were still a few species that caused evolutionarily inclined zoologists a bit of a headache—most notably the bower birds. Male bower birds decorate their bowers with color-specific odds and ends, and they arrange

⁸ See Dobzhansky (1937), Mayr (1942), Smocovitis (1996), and Cain and Ruse (2009).

the twigs and bits of color into amazing display arenas (Marshall 1954). Even as late as 1944, a popular article described the underlying function of the male's behavior as having "gone far beyond" a "purely utilitarian usage" (Chaffer 1944, 179). The author further posited that the birds derived "a great deal of satisfaction and pleasure in such activities" (Chaffer 1944, 180). Their penchant for play and aesthetically pleasing architecture set bower birds apart as prime candidates for wanton anthropomorphism.

Part of an answer came from an Australian earning his PhD in physiology at Oxford in the 1950s. Alan John "Jock" Marshall was fascinated by the possible correlations between bower birds' exotic behavior and their internal reproductive physiology. As a result of his research, Marshall suggested that the behavioral antics of male bower birds fulfilled a biologically necessary function-these behaviors helped both sexes come into sexual readiness at the same time (Marshall 1954, 69-71). Marshall considered himself "reasonably sure that neither intelligence nor conscious estheticism is involved in the bower birds' behavior. The bird's selection and placement of decorations in its bower is purely mechanical" (Marshall 1956, 52). The architectural marvel of a bower itself he attributed to a male's nervous activity as he waited for the females to become sexually responsive. Marshall earned the respect of his peers by providing an account of bower bird behavior that eliminated the need for recreation and aestheticism. After reading Marshall's book, one reviewer brought this point home by suggesting that bower birds provide "an extravagant example of the amazing complexity of behaviour which instinctive pattern can initiate and control."9

Like Marshall and the zoologists who preceded him, British theoretical biologist John Maynard Smith was interested in explaining the evolution of beauty within a single species, but he questioned whether such extravagant behavior and colorful plumage could be so easily dismissed as resulting from a need to coordinate the sexual readiness of males and females and to ensure species-appropriate couplings. Maynard Smith posited that the tail of the peacock could be explained only as an advertisement to attract the attention of females. He asked his readers to imagine bird plumage as a signal. If the point of the plumage was to function as a simple traffic sign—*to go to Brighton, turn right*—then the plumage needed to be easily recognized but not flashy, like the simple black and white coloration of black-headed gulls. Yet advertisements, he suggested—*Come*

to Brighton!—were only employed when the viewer had not yet made up her mind if Brighton was truly where she was headed (Maynard Smith 1958, 237, fig. 47). Maynard Smith argued that although many animal courtship displays could be reduced to functionalism, very extravagant displays should be understood instead as competitions for the attention of females. In other words, sexual selection was still needed. When a male failed to attract a female, it was not because of a lack of interest on the part of the male. The signal worked, but his lack of ability failed to arouse the female. Beauty and female choice were linked once again in his explanation of courtship behavior. Yet Maynard Smith's chapter on sexual selection failed to attract much attention when it was published in 1958. Not until fifteen years later did evolutionary explanations of beauty in the animal kingdom once again enter the zoological spotlight.

In the first half of the twentieth century, biologists depicted male behavior as the result of biological imperatives and rejected female choice in animals because of the cognitive functions they assumed were necessary for choosing a mate. If we take as our baseline the mechanical assumption that dominated much research in animal behavior in the first decades of the twentieth century (that animal actions should best be understood as evolutionary or psychological reactions to their environment rather than an active intervention), then the growing biological interest in sexually aggressive males competing for the attentions of females stands out as peculiar and in need of explanation. To understand this transformation in the field of animal behavior, we must turn to a slightly different community of scientists—those explicitly interested in the evolution of humanity.

Negotiating gender: Aggressive males and coy females

The 1960s was a decade imbued with violence. In the United States, the GI experience in Korea had presaged the discontentment and eventual anger with the war in Vietnam that now lit up television screens (Hallin 1986; Anderegg 1991). Civil rights protesters became increasingly frustrated with the slow pace of change, leading to urban unrest and riots in Watts, Detroit, Newark, Baltimore, and other major cities around the country (Gerstle 2001). Newspapers carried accounts of political revolutions in Africa, Asia, and Latin America. Combined, these events emphasized the importance of violence in structuring the political and social events of the day. Given this context, perhaps it is unsurprising that the rehabilitation of the animal mind began with aggression and began in anthropology.

⁹ M.G.B., "Review of A. J. Marshall, *Bower Birds*," *Biology* (June 1955); clipped copy in Alan John "Jock" Marshall Papers, Series 15, File 3, MS 7132, National Library Australia, Canberra.

Anthropologists in the 1960s self-consciously distanced themselves from racist accounts of human evolution common before the Second World War, hoping to replace them with a vision of humanity that held all cultures as equally complex and valuable (Proctor 2003). They also sought to understand why humans, of all animal species, were capable of killing each other (Carthy and Ebling 1964; Proctor 2008). Archaeologists, cultural anthropologists, and physical anthropologists produced a vision of humanity based on universal roles for men and women grounded in biological instincts. Man the hunter (or man the killer) provided food and social status for his family, while woman the gatherer (or woman the mother) raised the children and ran the household. Ironically, as anthropologists sought to distance themselves from overtly racist accounts of human evolution, they reinscribed sex differences as the biological basis of gender in all human societies (Haraway 1989).

In archeological reconstructions of human history, for example, the use and manufacture of weapons was often taken as a key process driving the continued evolution of human society. In 1959, Mary Leakey and her husband Louis Leakey shocked the world with their announcement of the 1.75 million-year-old Zinjanthropus in the Olduvai Gorge in Kenya-at the time, the oldest known "manlike creature" (Leakey 1961, 564; Ward 2003). In National Geographic Magazine, the Leakeys vividly described their reconstruction of human social evolution based on their archeological finds, accompanied by a six-panel, two-page image of the place of "Zinj" in human history (Leakey 1961, 570-71). According to the copy above the image, the first panel depicts the "earliest known hunters" from the site, who lacked weapons and survived by catching their food with their bare hands. In the second panel, Zinj brings down a zebra colt with a large wooden club, with the caption declaring him "a true man in the tool-making sense." The third panel portrays "the dawn of the spear," in which the putative descendants of Zinj work together to kill a large swamp antelope. The fourth panel represents a time of drought and climate change at Olduvai Gorge and thus pictures only small desert rodents. Hunters return in the fifth panel, as men and women gather around a large elephant-like creature stuck in the mud. The men carry spears and the women rocks. The final panel illustrates cheering men (still carrying spears) who have successfully stopped a giant ram in its tracks by throwing a Chellean bola around its front legs. Later in the article, Leakey (1961) described the virtues of the bola at greater length, calling it "an ingenious arrangement of three hide-wrapped stones connected by thongs" that when tangled around the legs of large running prey would bring them crashing to the earth (579). So what distinguished "true man" from his

bestial brethren in this developmental sequence of humanity? Not the ability to hunt or to plan ahead for the hunt, nor the ability to communicate with other members of the group for the purposes of hunting together—these activities were clearly depicted in the first panel. It was the manufacture of tools, and weapons in particular. As the rest of the article made clear, the manufacture of weapons and humans' evolutionary success was the work of men.

Contemporary research on extant so-called Stone Age cultures similarly emphasized the importance of male hunting and female domestic labor. For cultural anthropologists, it made sense to theorize about the culture of early humanity based on what they knew about human societies that had remained relatively free from contact with Western culture and technology (Clark 1968; cf. Berndt 1981). The pages of *National Geographic*, television specials, and books written by anthropologists claimed that each new tribe was more "primitive" than the last (Kirk 1969; von Puttkamer 1975). To be fair, these anthropological studies emerged out of concern that such cultures would inevitably be lost to the inexorable creep of technological progress through contact with the Western world. Yet these studies also reflected the same gendered division of labor as archeologists' visions of early humanity: man the killer, women the reproducer (Tanner 1981).

By the late 1960s, however, the idea of using "Stone Age" human cultures to stand in for man at the dawn of humanity became increasingly unpalatable to anthropologists. Both physical and cultural anthropologists saw the promise of using primate societies as a mirror or foil for reconstructing a universal human nature from the animal side, rather than the human (Lévi-Strauss 1968). Using primates rather than human cultures served to equalize all contemporary human cultures as more complex than early human societies. Additionally, if social behaviors were identified in the primate species that accorded with anthropological knowledge of human cultures, then it seemed likely that such traits were universal for all humanity. Two species dominated early discussions of primate behavior—baboons and chimpanzees.

To biological anthropologists like Irven DeVore (1965), baboons were the primate species that most closely adhered to the ecological environment that characterized the dawn of humanity, which made them an excellent source of information about our ancestors. Baboons—like early hominids, he suggested—lived partly in the safety of the trees and partly in the open savannah; they were highly social, and the males banded together to protect the females and young in the event of a threat (DeVore 1965). Male dominance and aggression appeared to structure their social organization even more than in humans. According to biological anthropologists Lionel Tiger and Robin Fox (1971), male baboons entirely controlled the hierarchical status relations of the group, while females bonded with their offspring. In Fox's writings in particular, the ultimate family unit was simply mother and child, while the males drove the intellectual evolution of hominids through their ability to negotiate their dual desires for sex with females and for social status derived from aggressive encounters with other males (Fox 1968). In a telling moment, Fox (1968) asked offhandedly about the other sex, "Was she simply a passive mechanism for passing along the genes of the big-brained males?" (93). His explicit answer provided only one way in which females might have contributed to the evolutionary progress of humanity: through concealed estrus, females made themselves constantly available for sex, thereby forcing males into the role of provider and into semipermanent familial relationships. Through the late 1960s, the primate literature largely concerned itself with how aggression and dominance relationships in males structured monkey, ape, and human societies and evolution (Zuk 1993).

Not all views of the barely human were quite so dismal. Jane Goodall, supported by Louis Leakey, believed that humans' closest living relatives, the great apes, were better models for human behavior than baboons (Strier 2003). This assumption underpinned Leakey's patronage of the young women who ventured into the wild to study great ape behavior in nature rather than zoos: Goodall's work with chimpanzees in Tanzania, Dian Fossey's research on upland gorillas in Rwanda, and Biruté Galdikas's studies of orangutans in Indonesian Borneo (Haraway 1989). Goodall's initial research painted a kinder picture of early humanity than that provided by DeVore's baboons. In her first article for National Geographic, Goodall suggested that chimpanzee babies played much like human children and that adult chimpanzees led rich emotional lives and communicated with each other through vocalizations (Goodall 1963). Perhaps most exciting were her discoveries that chimpanzees consumed meat and manufactured tools to help them eat. In the mid-1970s, however, Goodall witnessed the gradual extermination of one group of chimpanzees by another-a shocking series of events that made her question her previous assessment of chimpanzees as gentle (Goodall 1979). The aggressors were almost always males, and she concluded that war, kidnapping, and killing were not unique to humans. In unrelated circumstances, she also observed cannibalism on the part of three female chimps-for a brief period of time, they had eaten the babies of other members in the troop (Goodall 1979). Although Goodall painted the violent males as natural aggressors, she described this new horror as a psychological abnormality that the females in question were ultimately able to overcome. In the public sphere, these events further reinforced the notion that chimpanzees were strikingly similar to humans and that males were innately more violent than females. One headline even asked, "Chimp Killings: Is It the 'Man' in Them?" (Goodall 1978).

For universal sex differences to be found in humans, baboons, and chimpanzees, many anthropologists believed that there might be a biological explanation. DeVore, for example, suggested that sex differences in primates were associated with a nonarboreal lifestyle. He reasoned that as early human ancestors left the trees for the savanna, it became more important to protect the group, and selection favored larger and more aggressive males, as it had in baboons (DeVore 1965, 62, 182). Because males were in charge of protecting the group, a female did not need to defend either herself or her young, so she would never develop into "a fighting animal" (DeVore 1965, 38). This explanation also seemed to account for the less aggressive nature of the more arboreal chimpanzees described in Goodall's early research (see also Rowell 1974). Tiger, for his part, linked aggression with exclusively male activities: "Human violence is almost exclusively a male problem linked to our hunting history. ... War is the product of male bonding" (Tiger 1969, 42). By any account, sex differences were linked to a new understanding of males as driven by hostile encounters with other males, as possessing far more than a passive animal mind. Scientists still discussed female animal actions in terms of the nonaggressive, predominantly reactive behaviors that characterized descriptions of prewar animal behavior.

Sexual selection, in reference to either male-male competition or female choice, was not a common explanation for human or primate sex differences until the mid-1970s. At this time, field zoologists returned to a Darwinian model of female behavior that emphasized a continuity of choice across the animal-human boundary (Milam 2010). As a young maverick in evolutionary biology, Trivers (1972) provided an easily accessible theoretical basis for female choice as a mechanism of evolution by reviving the idea that females were certainly the choosier sex because they invested more in each offspring than did males. He reasoned that if females mated only once per mating season, then they would invest substantial energetic resources in variously producing eggs, giving birth, and raising offspring. As a result, females would be sexually coy-alternating bouts of intense courtship with periodic flights-to test the mettle of the males and gauge their ability to commit to offspring care (Trivers 1972, 148-49). Trivers suggested that because males could invest very little in their offspring, they had the opportunity to mate with multiple females

by abandoning each mate immediately following copulation. From the female's perspective, if a male would not engage in a prolonged courtship, then he was likely not to engage in extensive offspring care. Most animals exhibited some form of differential parental investment, and therefore most animals probably exhibited both female choice and male-male competition over mates. Trivers's point was twofold: that by playing coy, female animals actively chose better partners and that such female choice was far more common in nature than biologists had previously supposed.

Trivers attributed his interest in animal and human behavior to his involvement with a post-Sputnik federally funded curriculum reform program called Man: A Course of Study, or MACOS, in the 1960s (Nelkin 1977; Trivers 2002, 57). As part of the MACOS team, Trivers worked under DeVore (and educational psychologist Jerome Bruner) writing booklets about animal behavior and reproduction for a fifth-grade audience. The booklets created for the program spanned the animal kingdom and covered salmon, herring gulls, elephants, rats, chimpanzees, baboons, and more.¹⁰ After his experience at MACOS, Trivers decided to pursue a PhD at Harvard, where he worked closely with DeVore, and his early writings demonstrate his intellectual indebtedness to the anthropologists and zoologists involved with the MACOS project.¹¹ It is of little surprise, then, that Trivers's theories of sexual selection in animals tracked so well with anthropological theories of sex difference in primates and humans from the same time.

Trivers's conviction that female choice could play an important role in the evolution of animal and human mating behavior rather quickly caught a lot of attention. Entomologist Edward O. Wilson, also at Harvard, was thoroughly impressed by Trivers's ideas and based much of *Sociobiology*'s fifteenth chapter, "Sex and Society," on them (Wilson 1975). In the most recent introduction to *The Selfish Gene*, Richard Dawkins referred to Trivers as one of his "four intellectual heroes" and further suggested that "his ideas dominate large parts of Chapters 9, 10, and 12, and the whole of Chapter 8" (Dawkins [1976] 2006, xiv). It was through these two books that Trivers's research gained wider circulation among evolutionary theorists. The popularity of the word "coy," however, should probably be

¹⁰ Many of the educational materials for the MACOS program are available online at http://www.macosonline.org/.

¹¹ Trivers cites the work of anthropologist Asen Balikci (who developed films on the Netsilik), ornithologist William Drury (Trivers's mentor), anthropologist Richard Lee (a close collaborator of DeVore's who worked on the !Kung Bushmen), Lorna Marshall (who was approached about developing filmic materials on the !Kung Bushmen), and, of course, DeVore himself (see Trivers 1971, 1972).

attributed to Dawkins, as Trivers used the word only once and Wilson not at all. Dawkins went into great detail describing "coy" as only one possible mating strategy for females—the other being "fast"—in contrast to the "faithful" and "philanderer" strategies that males might adopt (Dawkins [1976] 2006, 151). Perhaps most interestingly, both Wilson and Dawkins painted sexual behavior as a negotiation between two equally active and obstinate partners—males and females.

The subsequent flurry of research activity among field biologists took for granted that female animals chose their mates and began to question the basis of that choice. Was female choice arbitrary (as supposed by Fisher's theory of runaway sexual selection), did females judge the genetic quality of males through the expression of their exaggerated trait, or did the trait itself correlate with some direct benefit to the female, like a highquality territory (Cronin 1991)? Biologists seemed unconcerned with the assumptions about aestheticism and mental capacity that had so preoccupied earlier generations, in part because they meant something different by female "choice" (Frankel 1994). Building on the same ethological framework Marshall used when discussing bower birds, evolutionary biologists began to suggest that naturally coy females were stimulated to mate by the male courtship displays (Hrdy and Williams 1983; Hrdy 1986). Human behavior, in other words, could be analyzed with the same behavioral tools developed to understand animal actions. Yet biologists' renewed interest in understanding the biological basis of human sexual behavior by comparing it to the courtship activities of nonprimates (following Wilson's sociobiological example) struck many biologists and humanists alike as a cavalier dismissal of those cultural and biological traits that distinguished humans from other mammals, rats, or even asparagus (Leonard 1969).

Throughout the 1970s and 1980s, feminist scientists and historians pushed against the sexual stereotypes embedded in these anthropological and biological theories (Hubbard, Henifin, and Fried 1982; Bleier 1984; Fausto-Sterling 1985). Elaine Morgan (1972) and Sally Slocum (1975) were some of the first women to vocally attack the sexism inherent in contemporary theories of human evolution and their overemphasis on hunting and meat. Critiques by others soon followed. Anthropologists Adrienne Zihlman and Nancy Tanner, for example, emphasized the crucial role of women in providing almost all of a group's nutrition through their gathering of foodstuffs and critiqued the anthropological theories of human evolution as failing to incorporate women's contributions to the ecological survival of the species (Tanner and Zihlman 1976; Zihlman 1978; Tanner 1981). Primatologists Sarah Blaffer Hrdy (1977, 1999b) and Linda Marie Fedigan (1982) suggested that mother love, far from being instinctual and kind, involved a great deal of learning and active negotiation with other members of the group to protect themselves and their young. The earliest of these critiques, by Morgan and Slocum, barely mentioned Darwinian sexual selection, whereas later evaluations of biological explanations of human difference devoted considerable attention to the theory. By the mid-1980s, referencing Darwinian sexual selection was necessary given its rising popularity (Hubbard 1990, 97–100; Cronin 1991, 113–230). Both Fedigan and Hrdy specifically took contemporary evolutionary theorists to task for appropriating Darwin's Victorian sexual stereotypes along with his theories, but for other scientists female choice offered a way of portraying females as active agents in their own evolution.¹²

The active rehabilitation of animal minds and actions may have begun with male animals and men, but it quickly extended to encompass the wide variety of strategies female animals and women might utilize to structure the societies in which they lived—from woman the gatherer to "woman the mate chooser, woman the mother, woman the aunt, woman the communicator, woman the power, woman the ritual actor, and woman the hunter" (Dahlberg 1981, xi). These newly created roles for female animals and women as active participants in their own evolution provided a place where questions of gender and sex were not easily resolved, a space where anthropologists and biologists continued to butt heads over the equally sticky dichotomy of nurture and nature (de Waal 1999). The biological females in these narratives ranged from "unaggressive, cooperative and bonded with other women" to "assertive, status-seeking, [and] dominance-oriented" (Zihlman 1985, 372).

In sum, the depiction of man as a "naked ape" in the 1960s rehabilitated the evolutionary and behavioral complexity of male animals to the detriment of their female companions (Morris 1967). Anthropologists and biologists actively appropriated coy females in the 1970s as a reaction to these earlier scientific theories about the biological basis of male aggression.

Conclusion

Although Darwin posited a continuity between human and animal minds, each in degrees capable of aesthetic evaluation and choice, by the first

decades of the twentieth century scientists had largely rejected the notion that any animal was capable of evaluative choice. Rather, they portraved animals' behavior as mechanical reactions to environmental surroundings and their evolutionary past. By the time Trivers, Wilson, and Dawkins refurbished sexual selection in the 1970s, male animal minds had already been transformed within biological anthropology. In the early 1960s, females may have waited for their big strong males to bring home the mastodon bacon in exchange for sex, but by the end of the decade they were actively engaged in elaborate courtship rituals that tested males' longterm commitment. As biologists and anthropologists increasingly emphasized animalistic instincts as important components of human behavior, they simultaneously began to see the antecedents of human behaviors in animal actions. These two trends of zoomorphism and anthropomorphism, respectively, were intimately linked in the 1960s. Aggressive males and coy females were thus active constructions of this scientific community, not passive importations from Darwin's century-old theory of sexual selection.

The legacy of female choice has been double-sided (Fausto-Sterling 1995).¹³ Critics of parental investment theory and sexual selection suggest that the gendered stereotypes embedded in evolutionary narratives of human behavior are cultural artifacts of questionable scientific value (for a recent attempt to dismiss sexual selection entirely, see Roughgarden 2009). Other evolutionary theorists see female choice as liberating. Biologist Patricia Gowaty, for example, argues that Trivers's paper "legitimize[d] the study of female choice" (Gowaty 2003, 901; see also Vandermassen 2005). Similarly, sociobiologist and feminist Hrdy (1999a) suggests that Darwinian theory, when applied carefully to human and primate populations, yields a picture far different than that provided by 1960s anthropology-females now possess as much agency in their behavioral choices as males. Trivers, Wilson, and Dawkins may have waltzed into a controversy with anthropologists over the cultural authority to pronounce on human nature (see Segerstråle 2000), but Gowaty and Hrdy both insist that they also (perhaps unwittingly) developed a robust and powerful framework for incorporating female choice into the evolution of human social behavior.

Female choice and other theories of animal behavior as keys to human

¹³ Since the 1980s, there has been considerable research on the evolution of sex differences in animals and people (e.g., Strum and Fedigan 2000; Clutton-Brock 2007). The journal *Integrative and Comparative Biology* also devoted most of an issue to the legacy of "Bateman's Paradigm" (2005, vol. 45, no. 5).

¹² See Fedigan (1982, 269–86; 1986, 26–32) and Hrdy (1986, 120, 122; 1999b, 22– 32); see also Hrdy's preface to the new edition of *The Woman That Never Evolved* (1999b), "On Raising Darwin's Consciousness" (xiii-xxxi). See also Tanner (1981, 1–14, 163–67) and Zihlman (1985).

nature maintain a powerful hold over our imagination not just because we recognize antecedents of our own actions in animals but also because we have been taught to see the animal within ourselves. Due to these earlier debates over the biological basis of human and animal behavior, we can reject simple masculine-feminine and animal-human dichotomies and instead recognize the multiple and diverse strategies and behaviors that constitute sexual identity in both animals and humans.

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