

Female Choice: The Theory of Mating

THE LARGE PINK REAR END of a female monkey bobbed through the juniper scrub. She was in estrus, or heat, and the swelling signaled to males, even those at a great distance, that she was ready to mate. She approached a young male, swung her rear into his face, and he mounted her. Both of them ignored the rattle of paper and scratchy pencil noises I made as I stood only five feet away, writing down their names, who started the interaction, and what happened once the sexual encounter ended. In 1986 I had come to this group of Barbary macaques, living on 20 acres of oak forest in southwestern France, to study female mating behavior. My job was to follow one of fourteen females for half an hour, several times a week, and note whom she mated with. The mechanics of this assignment were relatively easy because I learned early that Barbary females and males are clear in their choice of sexual partners. Barbary macaques breed only from September to January, when mating becomes the main activity of the adults. As females come into estrus, the skin on their hind ends inflates like a balloon in response to hormonal changes. These huge pink swellings indicate not only sexual receptivity but the fact that ovulation is imminent. A female Barbary selects a male by turning her hind end into his face, and if he's interested, they copulate. Some males wait for females to come calling, while other more assertive males approach females and give them a slight nudge from behind; if she's willing, they copulate. The female typically emits a loud, passionate call during the copulation, and then she spends a few minutes grooming him after it's over. The female always ends

the interaction by moving on, usually making a beeline to the next male.

My framework for this study was a theory of female mating strategies based on traditional evolutionary principles. This theory, called sexual selection theory, has a long history that includes the notion that females are discriminating sexual partners. Recently evolutionary biologists have discarded the image of females as passive creatures and have embraced the notion that females, just like males, not only have been selected to attend to their own reproductive interests during mating but also that they are assertive sexual beings. But, theoreticians point out, females, especially mammalian females, also invest more heavily in offspring than males do; females gestate and lactate while males are free to inseminate other females. The biological fact of this difference in investment suggests that females should be relatively careful about selecting potential fathers. Therefore female choice of a mate should be critical to female reproductive success. It might also be a potentially significant evolutionary force for males, affecting the passage of particular male genes on to future generations. The immediate goal of my study on the Barbarys was to gather enough data to test hypotheses, or expectations, about female choice of mates. I knew that they mated with several males, but presumably they were more choosy when ovulation was imminent. I intended to observe the choices my females made and to discover why they preferred certain males over others.

Initially, the behavior I gathered on Barbary mating fitted nicely into this model of female choice. Clearly Barbary females decide who gets to mate and when; they are perfect examples of the sexually assertive female primate. But at the end of the breeding season, 506 copulations later, I found myself questioning the current party line about female choice. Yes, these females were making choices, but they seemed to choose every male in the group, one after another, and there was no selectivity during the time when ovulation might be occurring. And as the days in estrus increased for any female, either by long cycles or by a greater number of cycles, I found a corresponding increase in the number of different male partners she copulated with. If Barbary females are supposed to be selective about which males would father the next batch of infants, I asked myself, why are they moving from male to male with apparent indiscriminate abandon? My data supported only the part of female choice theory

which indicated that females would be assertive sexual partners, but as for their choosiness—I was at a loss to explain why these females were more promiscuous than choosy.

I suspected that within the larger history of sexual selection and female choice theory were clues indicating why these females, and perhaps other primate females, didn't exactly fit current theoretical expectations. The day I watched a Barbary female copulate with three different males in the span of six minutes, I knew that it was time to reevaluate the current concept of female choice. Presumably the reason Barbarys didn't fit the standard model was because the model had some significant flaws. Thus began a historical search to understand why female choice theory said one thing and the females themselves did another.

Sexual Selection Theory

The theory of female mating strategies begins, as do all frameworks for animal behavior, with Charles Darwin. When Darwin published *The Origin of Species* in 1859, he sparked a revolution in the way we look at animal species, including humans. Species evolve, he suggested, because some individuals are more successful at staying alive and producing infants than are others. Traits and behaviors that aid an individual in survival and reproduction are selected over generations and mold the morphology and behavior of a species. But while promoting his theory of evolution by natural selection, Darwin was aware of a major flaw in his argument. If all individuals were selected by the same forces in a particular environment, why did males and female of the same species look so different?

He could account for some differences in male and female characteristics, such as ovaries, testes, sperm, and eggs, because those differences are necessary for conception and pregnancy to occur. They're what Darwin called "primary sex organs." If a species reproduces sexually, by definition there must be differences in the reproductive organs. Different primary sex organs have been selected by natural selection over generations to accommodate the complex process of reproduction by two cooperating parents. But more difficult to explain was the appearance of exaggerated features that pop up in only one sex and are often a hindrance to the individual. They appear at puberty yet have nothing to do with conception. And some-

times even when both sexes have the trait, it's exaggerated only in one sex or the other.

The peacock's tail is used most often as an example of an exaggerated characteristic found in only one sex. If you walk into the Burggarten in Vienna, Austria, a baby's plaintive cry often greets you near the statue of Mozart. You wonder if someone's neglecting a child, or if a baby needs a change. Strutting in front of the statue is a male peacock, and it's his cry that sounds like a wailing child. If disturbed, the male will stare you down, and then explode his tail into a dazzling fan of feathers like a Las Vegas showgirl. Walking nearby, probably unnoticed by you, is a possible mate of the male—the drab peahen. She's dull brown, she has no flashy tail, she doesn't strut or preen. She looks almost like a different species of bird. Or think about male and female lions. The females are smaller and they lack the regal brown mane of males. The male greater kudu of East Africa sports long twisted horns that reach two feet into the sky, while the female looks more like Bambi. If natural selection is operating on all individuals of a given environment equally, why should these males have things that females don't? Or put another way, why are males burdened with these extra accoutrements?

Darwin's answer to this question was simple. He suggested that males and females often look different, and sometimes behave differently, because they operate under different sexual pressures. Males must often fight one another to gain access to females, and, he proposed, because females are less interested in sex, males must spend time and energy attracting reluctant sexual partners. The exaggerated physical feature of males and their sometimes seemingly demented patterns of behaviors, like courtship dances, function primarily during the mating process. According to Darwin, these traits and behaviors have been "sexually selected" rather than naturally selected (1859, 1871). One can consider a trait sexually selected if it appears only in one sex, is used only during reproduction and aids the individual in gaining mates. This selection has nothing to do with the struggle for existence but everything to do with the struggle for passing on genes. Under the process of sexual selection some individuals gain the best, or the most, mates while others are less fortunate. Those who do best are the winners in the game of reproductive success, and their genes are passed on in higher frequency. And the traits or behaviors that helped them be successful competitors are passed on more frequently

than are the traits of the less able individuals. According to sexual selection theory, the "extras" seen on males, for example, aren't extras at all. They are weapons, armor, and ornaments that help in the battle of passing genes on to the next generation, and their sexual selection over time aids those winning males.

For Males Only

Most of what Darwin proposed as sexual selection makes immediate sense. If traits or behaviors arise only after males reach puberty, and if those traits help gain mates, those attributes will be passed on as successful males conceive more offspring than do males with smaller versions of the same trait. But how exactly does owning some sort of special equipment help a male?

Darwin offered two channels by which such traits could be passed on (1859, 1871). The first way, he proposed, is through competition within each sex, or what's now called intrasexual selection. The antlers of male deer are a case in point. When the rutting season begins for white-tailed deer in New York State, the woods often echo with the crack of antlers smacking together as two males crash head on. They are fighting for access to females who are in heat for only a short period. One male postures better than the other, one is able to push the other farther, and pretty soon the losing male backs off into the woods. The winning male then copulates with nearby females, distributing his genes, including the ones for good-sized antlers and strong fighting ability. The other male wanders through the forest, looking for another combatant with whom he'll have a better chance at winning. Darwin noted that competition within one sex for access to another sex would drive the exaggeration of traits that might help in competition, and he observed that males were most often the combative sex.

Examples of the intensity of male-male competition, and the real results of ousting the competition and gaining more mates, abound in nature. Massive horns in male bighorn sheep are used to push other males into reproductive oblivion; large canines are slashed about by a male baboon trying to keep other eager males away from his consort partner; bulbous throat pads wielded by male elephant seals protect them from the slam-dance of other males during their male-male battles on the beach. In all cases, males compete with one an-

other for females, while the females stand by waiting for the males to end the fighting and begin copulating. Such battles are especially fierce in arenas where females cluster together and come into heat simultaneously, creating a raucous male circus revolving around fertile females.

Nobody seems to ask much anymore why males have these battles: the evolutionary explanation is so clear. The battles occur too often, and the consequences of the skirmish is too predictable, to cause much theoretical bickering. Animal behaviorists have, in fact, proved one of Darwin beliefs. Many exaggerated traits seen only in males are used solely for mating and have been driven to exaggeration by sexual selection in the form of male-male competition.

For Females Only

The other channel suggested by Darwin that might explain why males and females look and behave differently is less clear. It's also the one most misconstrued by behaviorists and evolutionists—mate choice. Here Darwin was on shaky ground, and the past 120 years haven't improved on Darwin's initial thoughts very much. Darwin suggested that selection for some odd male traits, and thus the differences between males and females, could be explained by competition by one sex for the attentions of the other sex. This is now often referred to as intersexual selection, or mate choice. Most biologists agree that when it comes to choosing mates, females and their preferences will be more important in the evolutionary sense than the mate choices of males (more on this later). Thus intersexual selection is sometimes referred to specifically as female choice. In this scenario, females can be differentially attracted to some males over others, prefer them for some reason, and make an active choice for a certain type of male. Males with brightly colored features, pretty songs, or silly dances, for example, might win the favors of females simply because they catch the eye. There's no battle here, just attraction and choice.

Darwin based his ideas on female choice on the assumption that females are passive, less eager sexual partners. This supposed lack of passion on the part of females, he believed, explains why secondary sexual characteristics appear more often in males than in females. Exaggerated and unusual traits are needed only by the sexually potent

male sex because they alone were motivated to fight for, or attract, the opposite sex. Because males more often have secondary sexual characteristics, he reasoned, male-male competition in general must be a more powerful selective force than is female choice.

In his writings in *The Descent of Man and Selection in Relation to Sex*, published in 1871 to explain human evolution, human racial variation, and sexually selected traits, Darwin was very clear that female choice has only a minor role in explaining odd male traits. He devoted few pages to female choice, and bluntly called it not important. He also believed that female choice occurred only *after* males had battled it out. And even more depressing for females, he questioned their brain power to make decisions at all: "Hence the females, supposing that their mental capacity sufficed for the exertion of choice, could select one out of several males" (p. 259). He thought that females were rather passive about the whole thing: "Or she may accept, as appearances would sometimes lead us to believe, not the male which is the most attractive to her, but the one which is the least distasteful" (p. 273). Poor females are caught in this biological bind of having to choose a mate, then actually go through with a copulation. Female choice, for Darwin, evolved only because males need to attract females. Once again, he used sexual selection, this time female choice, to explain the appearance of male traits and behaviors. Ones that didn't evolve by male-male competition, he suggested, must have appeared as seductive attractors.

No one, including Darwin, was interested in females themselves. After all, scientists figured, fertile females can always conceive, and because they are apparently less eager for sex, females will always be in demand. Darwin even went so far as to suggest that females don't usually have any interesting traits to explain away because they just aren't endowed with the passions of males. According to Darwin, males are the eager, passionate gender, and thus only males evolved traits and behaviors to help them out sexually.

Sexless Victorian Females

This view of females, as passive and sexless, was accepted by Darwin and held by the scientific community for a century. Why was it so easy for scientists to accept a picture of females as asexual, passive individuals tossed about by the throws of sexual selection? The social

milieu, both then and now, has had an inordinate influence on how scientists view female behavior.

Like all scientists, Darwin was influenced by the Victorian world in which he lived—a world in which women of good breeding were dependent, passive, and supposedly asexual. Perhaps this background accounts for the following words he wrote about female sexual behavior: “The female, on the other hand, with the rarest exception, is less eager than the male. As the illustrious Hunter long ago observed, she generally ‘requires to be courted’; she is coy, and may often be seen endeavoring for a long time to escape from the male” (Darwin, 1871, p. 273). There were not many accounts of female mating behavior in those days—most observations were anecdotal or concerned domesticated animals that copulate only when allowed to, or forced to. No one really knew the “truth” of female mating behavior. The Victorians believed that only prostitutes, motivated by money, and nymphomaniacs, who were pathologically driven, eagerly engaged in sexual activity. What women Victorians felt, or what they did behind closed doors, is mostly a mystery (but see Brown Blackwell 1875, Burt Gamble 1894). Thus we can’t really blame Darwin for his perception of females—it was one shared by most of the English gentleman of his day, reinforced by the position of women in Victorian times as intellectually inferior but morally superior individuals whose role was to keep the household functioning (Sleeth Mosedale 1978).

Darwin was writing about the “nature” of female mating behavior without any concept of female sexuality. His views of animal behavior reflect what he saw at home, at least in a general sense. As Evelleen Richards, a feminist historian, points out, he was surrounded by a perfect Victorian family (1983). His wife, Emma Wedgewood Darwin, an intelligent and capable woman, bowed both to his scientific career and his illnesses. The women in Charles’s life were treated as inferior—his daughters were barely educated and yet the sons were well educated. Although Emma disagreed with his evolutionary views and worried about his lack of belief in God, this difference of perspective never got in the way of their relationship (Litchfield 1915). Interestingly enough, Emma was never converted to his views, although she understood his work (Richards 1983). And yet it was to Emma that Charles entrusted his draft of *The Origin of Species* in case he didn’t live to publish it. Emma maintained a household built around his health and wishes and he apparently worshiped her for that care.

Thus it seems reasonable to suggest that when Darwin wrote, "Man is more courageous, pugnacious, and energetic than woman, and has a more inventive genius," and, "Woman seems to differ from man in mental disposition, chiefly in her greater tenderness and less selfishness" (1871, pp. 316, 326), he was presumably echoing his own life and relationship with women. There was no contradiction in what he proposed for the natural world of female animals and what he saw in his immediate vicinity. Females were, by nature, coy, choosy, and very reluctant sexual partners.

Today we should know better, but the long arms of Victorian sexism reach into contemporary biology, especially in its thinking about sexual selection, female choice, and female sexual behavior (Hubbard 1979, Richards 1983). Although females are now seen as active sexual participants, there's always a footnote to their sexuality that makes females somehow "less sexual" than males. Modern texts in evolutionary biology and behavior concede that females may be sexually motivated, but a female's "need" to be choosy and not waste a precious conception renders her almost impotent. The issue now centers not on the rate of sexual interaction or the degree of sexual motivation by either sex but on the number of different partners. According to modern evolutionary theory, males "should" still copulate as often as they can and with as many partners as they can sequester, but females "should" be careful, choosy, less eager to mate. This view is, perhaps, only a modern, post-sexual-revolution version of Victorian sexism.

Female Choice—On the Edge of Biology

There's no need to take offense at Darwin's misogynist view—no one at that time really paid attention anyway. Alfred Russell Wallace, fellow evolutionist and well-known naturalist of the day, believed that Darwin was completely out of line for even suggesting female choice had any influence on evolution at all. The rest of the scientific community agreed with Darwin at least in principle: females had little influence on the mating game. And what Darwinian theory predicted was apparently seen in barnyards and forests: most male animals fought with one another, and the female reluctantly picked out a winning male to be the father of her latest brood. All thought of sexual selection, including mate choice, was therefore of little concern

to biologists for the next sixty years after Darwin's original formulation. It's impossible to figure out why some ideas gain prominence and attention and others don't. It's possible that evolutionists were so concerned with explaining and defending the theory of natural selection to the world that sexual selection, let alone female choice, was not the major focus for biologists (Maynard Smith 1991).

During the 1930s and 1940s, when geneticists drew up the synthetic theory of evolution and Darwin's evolutionary theory was finally combined with modern genetic theory of the modes of inheritance through chromosomes and genes, sexual selection and mate choice came up for a temporary breath of air. A mathematician, Ronald Fisher, focused on female choice for a few pages in his book *The Genetical Theory of Natural Selection*, published in 1930, but like Darwin, he was interested in female choice only insofar as it influenced the evolution of male traits. He began with a little hand slapping. Fisher maintained that naturalists, who were still not particularly interested in sexual selection theory anyway, had become so focused on differentiating male-male competition from female choice that they'd lost sight of the unifying principle underlying sexual selection—competition for mates (1930). The distinction between the two types of sexual selection, male-male competition and female choice, had become important, he said, only because of the thorn of female choice. Wallace had dismissed it, and nobody was particularly convinced that females might have an effect on the evolution of male characteristics at all. But Fisher's major contribution to female choice theory, as we know it today, was the insistence that certain requirements must be met if mate choice, particularly female choice, is to have an evolutionary effect. First, the preference must occur consistently. It doesn't really matter if one female chooses this and another chooses that: females in general must prefer one type of male for their choices to have an evolutionary effect. Second, the preference must confer a reproductive advantage to the chosen individuals. It's not enough to demonstrate that most females reach out to some males with a particular trait for that trait to be favored by sexual selection; the said males, favored by most of the females, must also have lots of offspring. He saw the process as a kind of coevolution—males have a trait, females like it and mate with them. Females then have sons with the trait and daughters with the preference. The trait and the preferences are in-

herited together over and over, coevolving with each other (O'Donald 1980).

Fisher also reiterated another point made earlier by Darwin: there must be checks and balances in the sexual selection system. If females are drawn again and again to males with an outlandish trait, the trait would eventually appear larger and crazier after many generations of favoring only those at the outer limits of exaggeration. The reason that sexually selected male traits haven't gone wild is that natural selection waits in the wings, ready to end the path of runaway selection and keep things in moderation. For example, males might evolve giant canines that aid in their battles over females, but eventually these big teeth would get in the way of normal eating, and regardless of the advantage of large canines to male-male competition, the limits of natural selection would be reached. Thus natural selection is the brake that keeps the runaway train of sexual selection from going off the evolutionary cliff.

The direct relationship between female choice and the exaggeration of a male trait has been empirically demonstrated for African widowbirds by Malte Andersson (1982). Male widowbirds are black and have red epaulettes. The females, by contrast, are dull brown. The males also sport an extremely long tail, about 50 centimeters, while the females have a more normal-sized appendage. In an ingenious experimental design, Andersson added pieces of tail feathers to some males and shortened the tails of others; for controls, he left some males as they were or clipped and then glued back the same tail segment on the same bird. Andersson found more new nests in territories owned by males with artificially lengthened tails. He also shows that males didn't use their exaggerated tails in male-male competitions, and he concludes that the only explanation for the evolution of long tails is female choice. Female widowbirds consistently choose males with the longest tails, thus demonstrating the power of attraction of long tails to the opposite sex, although the elongated tail in and of itself has no real value to males or females and might even hinder the male.

Fisher's work might have led to a renaissance for female choice theory, but still the times weren't ripe. No one had yet conducted a long-term study of female behavior, and there were few studies of mating behavior in particular. But Julian Huxley, the zoologist, took

up the gauntlet in 1938. In two important papers Huxley wrote a thorough evaluation of Darwin's original sexual selection theory (1938a, 1938b). Like any good scientist he questioned Darwin's assumptions. Huxley proposed that most male characteristics, be they aggressive displays or morphological features aimed at competitors, could be explained as adaptations that "promote the union of gametes." And like a good scientist he also tried to give this process another name—epigamic selection—to underscore the need for these features in reproduction. No one uses this term today because it's superfluous. He really meant selection for features needed for male-male competition, just as Darwin did. While Huxley was grinding away on the details of male-male competition, he seemed to dismiss female choice. Huxley, too, believed that mate choice, and this meant female choice, was a minor evolutionary force. He explained most ritual courtship displays as events in which males rev up their sexual engines rather than try to win the favors of females. Although these papers are considered important for the history of sexual selection theory, they are, as the geneticist Peter O'Donald says, "hopelessly confused" (1982). More to the point, these papers added nothing to the concept of female choice in particular and actually sidetracked researchers even farther away from female mating behavior. It would be almost twenty years before an insightful biologist began to wonder seriously about the female role in mating.

The Unheard Champion of Female Choice

In the 1950s, John Maynard Smith, a biologist at the University of Sussex, began working with *Drosophila*, the tiny flies that invade your rotting fruit in the summertime. Although Maynard Smith was initially interested in male fertility and the mating process in general, his early lab experiments on flies resulted in some unexpected information about female mating behavior.

In one of his first experiments, Maynard Smith worked with an inbred strain of flies in which many of the males became infertile because of their inbred heritage; the overall population of male fruit flies varied in relation to the degree to which each could fertilize eggs (Hollingsworth and Maynard Smith 1955). The variation in potential

male fertility also fortuitously led Maynard Smith down the female choice path. During the experiments, he noticed the ritualized courtship dance of male and female flies. Females and males face each other and dance right and left in a coordinated fly tango. At first, when females bobbed right and left in front of a courting male, Maynard Smith assumed that the females were trying to get away. But experiments with wax models of female flies in another laboratory showed that female participation in the dance was actually required for mating to proceed smoothly. More important, Maynard Smith noticed that the female often started dancing first, just to see if the male could keep up. When faced with inbred males, who were clumsy dancers with bad timing, females turned away. These inadequate suitors sometimes tried to mount females, but they were often too far forward or too far back, and the female would eventually kick them off altogether. As Maynard Smith put it for these poor males, "The spirit is willing but the flesh is weak" (1955, p. 272).

He proposed that the female dance, which must be closely followed by the male partner if he wants to achieve copulatory success, evolved on the female's behalf. In other words, she judges a male by his dance, and the dance is a true indicator of male fertility. Presaging the words of biologists who were still in grammar school, Maynard Smith predicted that females might have interests of their own on which they base mate choices. Second, these female choices might have an effect on the appearance of male characteristics and behaviors. This was a new kind of female choice, one not centered on the importance of male-male competition or on the notion that females mindlessly choose males with the wildest displays. This was not Darwinian or Fisherian female choice in any sense because it viewed choice from the female side. Maynard Smith was suggesting that such choice also had a major impact on the evolution of the species.

Unfortunately, no one was listening. Maynard Smith recently wrote: "When, in 1956, I published a paper showing at least to my own satisfaction, how female fruit flies choose males, I do not remember receiving a single reprint request" (1991, p. ix).

It would be twenty more years and the one-hundredth anniversary of Darwin's concept of sexual selection theory before anyone seriously considered females, and female choice, as a powerful selective force.

The Feminist Revolution in Animal Behavior

The average person on the street is not aware of revolutions in academics. No one is killed, no one dies, although many a reputation can be wounded. In the late 1960s and early 1970s, a major change was in the wind for behavioral biology. Studies of animal behavior before that time had been thought of as a kind of natural history—watch animals, describe what they do, paint a picture of the animal's life. But as I mentioned in Chapter 3, several biologists during the 1960s had begun to look at evolutionary explanations for behavior. Eventually the discipline of sociobiology, the study of the biological basis of social behavior, was born. The tenants of sociobiology are simple. Patterns of behavior, just like skeletons and muscles, have evolved by the rules of natural selection and sexual selection. Individuals who behave in ways that improve their reproductive success pass on more genes than do those who behave in ways that don't help them pass on genes.

Females, perhaps, benefited most from this new perspective. Before the days of sociobiology, female animals were considered only as mothers, and no one really thoroughly investigated what else females did with their lives. The new evolutionary framework allowed for hypothesis building, and females were part of the equation that would eventually explain patterns of behavior. This reorientation toward females also caused sexual selection theory, and female choice theory, to gain attention.

Interestingly enough, this flowering in the history of female choice theory isn't just a shift in an established scientific paradigm. It can also be accorded to major changes in the social milieu of the very biologists who were developing theories of animal behavior. In the 1960s and 1970s, two other revolutions were in progress in Western culture, the feminist revolution and the sexual revolution. Although there's no way to prove that an orientation toward nonhuman female behavior and sexuality was initiated by these not-so-subtle cultural forces, no one can deny that the new social freedoms for women in the Western world had some sort of influence on the new chic position of female animals in behavioral studies (Andersson and Bradbury

1987). In addition, more women were entering the sciences, and although not all women behaviorists studied females, and many men did, there was an air of refocus.

But don't be deceived. Academic feminists of the time did not sanction this reorientation and they did not clearly understand (nor do they now) biology's role in explaining female behavior. The anthropologist Sarah Blaffer Hrdy wrote about her graduate education at Harvard in the 1970s and the odd position of being a feminist studying biology: "Within the Harvard of that time there was no overlap at all between feminism and evolutionary biology, not even a common language. Feminists were outraged at what they took the sociobiologists to be saying, and the sociobiologists were mystified to discover that feminist were demonstrating at their lectures. As a woman in the midst of all of this, I felt torn and often quite alone" (1981a, p. ix). Studies of female animals were gaining ground, but many things about the "natural" behavior of females disturbed their human cousins. For example, field and lab studies showed that male animals were often highly aggressive and dominant to females. But what the feminists were slow to hear was the female power inherent in many behavioral descriptions. Blaffer Hrdy's book *The Woman That Never Evolved* was revolutionary for its time because she said that female primates were not passive individuals waiting for males to finish battles. Instead, she painted a picture of competitive, strategizing, sexually assertive creatures (1981a). According to the new evolutionary biology of those years, female primates are the same as males in that they have been selected to act in ways that improve their reproductive success. At the same time, sociobiology showed that females are also different from males because the constraints of pregnancy and parenthood have molded very different creatures. Females and males are apples and oranges thrown into the same basket.

And in the midst of the new perspective on behavior, where was the issue of female choice as a potential evolutionary force? Gaining ground.

The major boost to female choice theory had occurred in 1972, when Bernard Campbell proposed an edited volume to celebrate the one hundred-year anniversary of the publication of Darwin's *Descent of*

Man. Although many papers in this book are important and interesting, none has become more famous in biology circles than Robert Trivers's work on parental investment and sexual selection (1972). Trivers followed John Maynard Smith's lead of two decades earlier when he turned his attention toward female choice. But he also added a spin to female choice which may have had serious, and I think somewhat negative, effects on the way biologists view female behavior.

Two Kinds of Choice

Trivers explained something Darwin couldn't. When Darwin first thought of sexual selection and female choice, he reasoned that the passionate males would be the fighters and the less eager females the choosers. Trivers, with one hundred years of biology under his belt, was able to support Darwin's dichotomy on a purely biological basis without making reference to passion. Trivers pointed out that males produce mass quantities of highly mobile gametes, called sperm, and because these cells are available in the millions, males have the ability to inseminate many females, so that each male's potential for passing on genes is extremely high (1972). Females, on the other hand, normally produce few gametes, even if they have litters or broods, and those eggs are precious reproductive commodities for females. This division makes evolutionary sense and can easily be applied to Darwin's original division of the sexes in terms of sexual selection; males will compete and mate indiscriminately and females will be choosy because of their differences in reproductive potential. But Trivers went further. He pointed out that beyond the gamete level there are significant reproductive differences in males and females because the two sexes differ in the amount of parental care they invest in offspring. Each individual has only so much energy to expend on bringing up offspring. For most females, especially mammals, reproduction includes not only the production of fewer gametes but also gestation, nursing infants, caring for them, and protecting offspring from predators. A female's lot, or better, her evolutionarily selected strategy, is such that she must invest heavily in infants. Males, on the other hand, can go about spreading sperm as long as there are females to mate with and infants don't need any fathering. Females are the

limiting resource in this mutual scenario because, after insemination, females must drop out of the mating game and attend offspring. Males, on the other hand, will always be fighting over females because males need females not only to bear but to bring up infants. Trivers didn't address the origins of this reproductive difference, he just pointed out the consequences—females should be extremely choosy about whom they share their genes with.

Darwin and his colleagues originally believed female choice to be a simple matter: females look out for the right species, the right sex, and the right age male—perhaps waiting for the battle winner or choosing a mate with an odd trait. Darwin certainly never dreamed of the kinds of discriminations Trivers proposed. Female choice, from 1972 on, imbued females with the power to choose the “best” males on every level—genetically, physiologically, and behaviorally.

Trivers's work is important because it veers away from the established view of female choice. Previously, female choice had been used to explain odd male characteristics; Darwin, Huxley, and Fisher never considered the possibility that females might have interests of their own. After all, they thought, an estrous female can always conceive because there are zillions of sperm lurking in every corner. Trivers, surely influenced by his own social milieu, pointed the spotlight on females themselves. Under Trivers's scheme, a female's choice might also drive the evolution of odd male characteristics, but it might also be a choice made by the female in her own best reproductive interest.

Contemporary Female Choice Theory

This simple concept, now called “female choice,” has riveted researchers in animal behavior since the early 1980s. Behaviorists find it difficult to demonstrate, and yet we intuitively know that females somehow influence who gets to mate and when. We have usurped Darwin's original meaning, added a few twists of our own, and ended up completely confused by the whole issue. In essence, we have made “female choice,” as an evolutionary concept, as illusive as female sexual behavior was to the Victorians.

The result of Trivers's theorizing, in particular, is that we have two ways of looking at female choice (Heisler et al. 1987), although these

are usually lumped into the general heading “female choice,” and most biologist often don’t see, or distinguish, the difference between the two types. In the first kind of choice, proposed by Darwin and refined by Fisher, females make choices, for whatever reason, and after many generations the male trait and the female preference co-evolve until the trait is exaggerated and useless. It doesn’t really matter why the female chooses a particular male, only that she and her female colleagues keep on doing it. Eventually the male trait no longer has any fitness value to either partner but males keep up the waving and females continue to choose. The result is the exaggeration of a trait that means nothing in terms of reproductive value or as a sign of male vigor. I call this way of looking at female choice “Fisherian” choice.

Some biologists see this approach to female choice theory as “non-adaptive” (Kirkpatrick 1987), because such choice can lead to the development of useless traits or to no development at all. This point that the female action does not necessarily influence the male trait per se is powerfully illustrated by Andrea Basolo’s work on green swordtail fish (1990, 1991). Given a choice, female swordtails consistently choose males with longer tails, and Basolo shows that only the length of the swords, and no other perceivable male traits, has any effect on female preference. But more important, she shows that females in ancestral swordless platyfish also prefer sworded males when conspecific males appear with artificially attached swords. In spite of this inherent preference among platyfish females, however, there’s been no evolutionary change in the morphology of caudal fins in male platyfish. Basolo’s research establishes the existence of a female mating preference that has had no apparent evolutionary effect on male phenotype. In such cases, “female choice” isn’t synonymous with intersexual selection. The demonstration of a historical evolutionary *enhancement* of a male character, not the existence of the preference, is the first stimulus for considering sexual selection as the mechanism of change. Mathematical models have used this type of female choice to test how male traits might evolve (Boak 1986, Kirkpatrick 1982, Lande 1981, O’Donald 1980, Seger 1985), but models don’t explain what females and males actually do, or how they pair off and mate.

The other way of looking at female choice, by which females have

their own interests in mind, and the type of choice most biologists now attend to, is what I call "Triversian" choice: females make choices based on what they perceive as best for them, choices that may not have any effect on males. The only time a male is affected, as in the Fisherian sense, is when those traits somehow have a link to the fitness of a male (Small and Palombit ms., Small 1992b).

For an example of the subtle difference between Fisherian and Triversian female choice, we turn to pheasants. Torbjörn van Schantz and colleagues from the University of Lund, Sweden, have shown a direct connection between a male trait—the spurs on the legs of male pheasants—female choice, and improved reproductive success of females (1989). They factored out male size, wing span, territory, and age by changing the kinds of males available to females. Only spur length was of consistent importance to females. And females who mated with long-spurred males hatched the largest clutches. In other words, if a male trait is correlated with health and vigor, and females are attracted to that trait, their choices will affect the reproductive success of the females and the evolution of the male trait. In this case, the genes for male spur length are passed on to her male offspring, but this fact is almost incidental to the fact that females who choose these males have bigger clutches. These traits are called "truth in advertising" on the part of males. But from the perspective of the female, the effect of a choice on male traits is not important. She is driven only by the result of that choice for her offspring. From this perspective, the male trait, and how it evolved, is secondary to the motivation of the female making the choices.

The proponents of the "truth-in-advertising" school of thought, also known as "the good genes" hypothesis (Kirkpatrick 1987), look at female choice from the purely female point of view, that is, the way females might look at potential mates. They believe that any characteristic a male waves purposely at females is really an indicator of male vigor (Andersson 1986, Hamilton and Zuk 1982, Kodric-Brown and Brown 1984). For example, a male deer with the biggest antlers is probably the healthiest and will pass on the best genes. Or the bright coloration of male birds can be explained as a neon sign selected by female choice because colorful males have fewer parasites and females are attracted to their brightness and good skin condition (Hamilton and Zuk 1982). This perspective suggests that females make

fine-grained discriminations among males and choose those who potentially have the best genes. But males can play this game too. One evolutionary biologist, Anton Zahavi, has suggested that males sport these odd characteristics only as a metamessage to females (Zahavi 1975). According to Zahavi, a male dragging a huge tail is shouting, "Hey, honey, look at me. I can walk around *and* carry this unbelievable thing. Mate with me." The only truth in his advertisement is that the male can operate with a giant handicap.

Both these two types of female choices, or two ways to analyze why females make certain choices, have the potential of affecting male characteristics, but the "Triversians" don't really care. For them, if a female makes a choice of any kind, regardless of how it affects the evolution of male traits, it's female choice. And many biologists have even forgotten the connection between female choice and the possible evolution of male traits. They focus solely on female choice for improvement of female reproductive success. Patterns of behavior or attributes of males that might help this reproductive success, not exaggerated male traits are the focus of many studies today.

Some male traits may act as neon signs to females, and the appearance of these traits has certainly been affected by female preference over time. But both theory and real studies have made the issue of choice even more confusing. Many studies have shown that females do choose males for certain traits and presumably drive the evolution of those characteristics. To name but a few, female preference and choice can explain the loud courtship call of túngara and cricket frogs (Ryan 1983, 1990), male coloration in ladybirds (Majerus et al. 1986), or the pattern of orange spots on male guppies (Farr 1977, Houde and Endler 1990). But a direct connection between female choice and improved female reproductive success in the Triverian sense has been shown in only a small number of species such as pheasants and *Drosophila* (Partridge 1980, von Schantz et al. 1989). For most species, the impact of any kind of female choice is still so much theorizing. And certainly no one has clearly demonstrated how female choice might influence the evolution of a particular pattern of *behavior*. Can female choice select for the pattern of behavior called male "friendship," or bring about the evolution of paternal care?

We're actually unsure what females want, how they choose, and if they do make choices, how those choices affect individual female

or male reproductive success. So far, the theory behind female choice has been basically a road map used to initiate studies. More interesting information, and intellectual growth, has come from what animals teach us with their behavior beyond the theoretical predictions. The original theory of female choice, and its development, has been merely a steppingstone to understanding what female animals really do when they mate.

The Art of Choice

The verb "choose" is defined in Webster's dictionary as "to take as a choice; pick out by preference from all available, select." When the word "choice" is used to describe human behavior, we assume it always includes some sort of decision-making process. A person is presented with a number of options, evaluates those alternatives, and then makes the selection. We Westerners like to believe that all our choices are conscious; we firmly believe in the concept of free will, and the idea that some decisions in life are unconscious often implies a lack of freedom. And worse, we'd hate to think some things were "fated" and predictable, and thus also out of our control! But humans, like all animals, make both conscious and unconscious choices, and some choices have a foot on each level of consciousness. For example, it's reasonable to suggest that choice for a certain sandwich at lunch is a conscious choice, whereas choice for a particular mate is probably more unconscious.

But when the word "choice" is applied to animal behavior, we're at a loss to describe exactly what the animals are doing. The animals can't explain their motivation in words, and we observers can rely only on their behavior as a clue to their preferences. In most studies of female mate strategies authors provide a qualifying statement to the effect that their subjects are not making "real decisions," but that natural selection has operated to favor those females who prefer mates with certain qualities. The action then is presumably unconscious. Only the primatologist Robin Dunbar, in his volume on gelada baboon female behavior, is straightforward in his opinion that the animals are making conscious decisions about their social interactions: "I shall make frequent use of the language of conscious decision-making. . . .

I do so partly because this is much the easiest way to discuss the animals' behavior, but also partly because fifteen years of field work have made it abundantly clear to me that strategy evaluation is precisely what the animals are doing" (1984, p. 4). It's probably more useful to avoid the semantic machinations involved in deciding whether mate choice is conscious or unconscious. After all, we'll probably never know how animals think or how they make decisions, and evolution doesn't care anyway. Evolution acts only on the consequences of the decision.

We get into another semantic puzzle when authors use the word "preference." While "choice" indicates an action that can be observed and measured, "preference" denotes desires that may or may not result in choices (Heisler et al. 1987). For example, a female might prefer the most dominant male, but she makes a choice for a less dominant one because she's afraid of the bigger male; she may prefer a particular male (desire or motivation) but be unable to gain access to that male (the choice itself). So far we know only that female primates do make choices, be they conscious or not. The whys and wherefores of those choices, and the preferences they're based on, are more difficult to figure out.

Unrequited Needs

Probably the major reason female choice theory has developed along such a twisted path is the nature of the behavior. A female's selection of a mate isn't a simple matter of evaluating a number of possible options, deciding on one, and marching up and taking him. Any female choice of a mate is complicated by the fact that she's interacting with males, and those males have agendas of their own. Not for one moment should we forget that female mate choice operates in tandem with male mate choice. Unfortunately for females, and those who observe nonhuman primates, the presence of males can have a domineering effect on potential female choice. With humans, we can at least ask a hypothetical question about what a woman might want from a mate if she lived in a free-for-all female-choice world. Asking nonhuman primates is more difficult; we must look for subtle clues.

Barbara Smuts, an anthropologist, has recently suggested that much of primate mating, including human mating, occurs in an arena of male sexual coercion laced with violence, and thus coercion may be true for other animals as well (1992, Smuts and Smuts in press). She illustrates her point with chimpanzees. Although the majority of chimpanzee matings occur opportunistically, females often follow males on safaris away from the group, and a third of all conceptions occur during these exclusive matings. Males try to tempt females away, but sometimes they refuse to go; the ardent male may threaten the female and attack her (Goodall 1986, Tutin 1979). Females usually respond to these attacks by following the male in question. Smuts's point is that these scenes may indicate long-term tension between males and females which place females at risk from coercive males. It may be that even when females seem to wander off under their own free will, they are responding to previous attacks and are following only out of fear. Attacks by males on females in many species increase during breeding seasons, and males routinely threaten females in estrus. Male macaques, for example, routinely interrupt consortships between estrous females and males lower in rank (Hanby, Robertson, and Phoenix 1971, Huffman 1987, Manson 1991), although females usually resume the consortship posthaste.

In one study, the possibility of pure choice by females without male interference was tested in the laboratory. Pigtail macaque females were trained to hit a switch when they wanted to release a male into their presence (Eaton 1973). Females released males most of the time, but seemingly for purely sexual reasons: the females copulated throughout their cycles with any male they set free. They were also rather easy with their favors—most females released three of the seven possible males they were paired with. And when one male was repeatedly aggressive toward the subject females, they just stopped releasing him. The point is, it's hard to tell the motivation of a female, and her preferences or choices, when there are males involved who are often larger and stronger and tend to bully their way into matings. In these situations, according to Smuts, free choice for females may be an illusion.

Females may also be frustrated by their own kind. If we assume that each female is out to improve her individual reproductive success, it follows that competition among females may occur, especially if

preferred males are in limited supply. In seasonally breeding groups, there may not be enough males to go around, and it's possible that females mating at a high rate will deplete the sperm supplies for other females (Small 1988). Two studies have given preliminary evidence that this is true. A comparison across eighteen field studies of baboons shows that when the ratio of males to females decreases, the birth rate declines (Dunbar and Sharman 1983). Similarly, in a captive group of bonnet macaques, female fertility was lowest in the years when the ratio of females to males was the highest (Silk 1988).

Because the prevailing sentiment concerning male sexual behavior is that males will copulate at the drop of a hat and that any estrous female can conceive, why are some females not conceiving? Non-human primates show us what many single women in America today already know—sometimes it's very difficult to get a date. Female rhesus monkeys and baboons often present to males, a clear sign of preference and choice, but males regularly refuse (Lindburg 1983, Saayman 1970, Scott 1984). Lion-tail macaque females, especially sub-adults, share this rejection. Females of this species initiate almost 70 percent of the copulations but only 59 percent end up in mounts (Kumar and Kurup 1985b). No one is sure why these males refuse, inasmuch as sperm is supposed to be so cheap, but males often ignore estrous females. Thus female choice is frustrated by male whims.

Are the females really free to choose? Are they coerced by males and shoved aside by other females into relationships that aren't particularly favorable? Once again we must ask, when females have preferences, are they allowed to make choices?

Given Their Druthers, What "Should" Females Want?

The current consensus about the "shoulds" of female mate choice is very clear—females bear few offspring in which to pass on genes, and each is dependent for a long time; thus they should be careful when choosing fathers for those infants. Female choice for her own reproductive well being, when it occurs, should reflect the reproductive interests of females.

From an evolutionary standpoint, certain male characteristics should be critical to female choice (Halliday 1983). Although the im-

portance of each variable changes with the phylogenetic, ecological, and social makeup of each species, it's possible to think through several attributes of males that we assume could be important.

The first thing a smart female animal should look for is a male of the same species and the right age. Some behaviorists think that the best thing a female can do is find a male with "good genes." Such a selection sounds like a reasonable expectation, and truth-in-advertising would certainly help females figure out who has good genes. But the argument for good genes is confusing because we define "good genes" as those that are passed on and, at the same time, suggest that good genes are the reason that an individual is reproductively successful in the first place. And no one seems to know exactly what "good genes" really are. Perhaps good genes are those that make for a strong immune system that resists diseases and parasites (Hamilton and Zuk 1982), or maybe good genes are those that help a future infant escape from predators. Unfortunately there's no clear way to define good genes, not even for our own species, because "good" is relative term that fluctuates with environmental conditions. Certainly no research on primate females has suggested that female primates have made specific choices based on a male's genetic quality. Females might also choose for male status or the goods he might provide, such as territory, food, or parenting.

It might also be advantageous for females to prefer familiar males over unknown males, and such a choice would be possible in groups in which males hold tenure for long periods or don't emigrate. But a penchant for the familiar might be overshadowed by a taste for the unknown—the novelty factor. Females are presumably interested in these males because they are different and attract attention. This selection for novel males may have evolved to avoid inbreeding. If a female is attracted to an unknown male, most likely he won't be related to her. A female might also find genetic variability for each conception when she seeks out novel males one year after the next.

And finally, we must consider the possibility of popularity. Humans base many of their mate decisions on "attractiveness." The components of beauty are distinctly different from culture to culture, and they change with time. We can't, however, dismiss the possibility that nonhuman primates, especially, have some concept of attractiveness, or beauty. In fact, many of the choices made by nonhuman

primate females which seem unexplainable to human observers may fall into this category. One male in my group of Barbary macaques was repeatedly the target of female attention. To my human eyes he seemed a brute—he bit females and never engaged in mutual grooming. But the Barbary females saw in him “a certain something” only a macaque female could explain. His rate of copulation was higher than that of any other male.

If paternal ability, friendship, or unfamiliarity are important to females, recognizing individual males and their behavior would be paramount to the choosing females. This view suggests that unlike Darwin's females, described as dunderheads unable to deal with decisions, females are “socially intelligent” (Cheney, Seyfarth, and Smuts 1986, Small 1990a). They must have the ability to discriminate among males, repeatedly interact with the same males, and possess a large memory for sorting social information and understanding a social network. Because primates are known for just this type of mental processing, this suggestion seems reasonable.

What we don't know is whether female primates in particular actually *have* any of these proposed druthers. Researchers have painted a female choice world in which female primates have read the literature on what they “should” want. Our most difficult task is understanding what they *do* prefer, and exactly how they are motivated to make choices based on those preferences.

Female Choice among Primates

Primates, with their big brains, high intelligence, and flexible behavior, are likely candidates for studies of female choice. Whatever the theory, thirty years of primatology, including laboratory and long-term field studies on females, have shown that female primates are active participants in the mating game. They often initiate sexual bouts, and they walk away from male partners as well. Females are highly sexual, mating not just for conception at the moment of ovulation but repeatedly during the estrus cycle. They are clearly sexually assertive, but we still don't know what the evolutionary effect of that assertiveness might be, or why it evolved. And we aren't sure how a female primate's choice of a partner has shaped the evolution of primate mating systems.

To look for the original kind of female primate's choice, we have to step back and see if there's something to look for in the first place. Recall that Darwin and Fisher and others after him were trying to explain the appearance of odd traits in males. Let's broaden that to say we're trying to explain traits that appear in one sex and not the other. Did a trait come about because the opposite sex liked the trait, selected it over generations, and drove it to extreme proportions? Although this "Fisherian" type of female choice has been used to explain such obvious things as the peacock's tail, we're hard pressed to find such extreme sex-distinguishing traits in primates. Male primates are usually bigger than females, but this larger size is probably due to intense pressure on some males to compete with other males during mating. In other words, large male size has been sexually selected, but through male-male competition. Male baboons have huge canines, but females have pretty big ones too, and the male exaggeration is also due to male-male fighting. There are only a few examples of male traits which might need some Fisherian female-choice explanation. For example, several lemur species come in sexually dichromatic colors (see Figure 3). The males are one color and the females another. Because the color within a sex—male black lemurs are all black, whereas their female counterparts are all brown—is uniform, this trait probably didn't evolve to help males in fighting. It may have evolved by female choice, even if the color difference has nothing to do with male quality. Another possible example is the brightly painted red-and-blue-striped faces of male mandrills: just as with many bird species, only males have the bright faces while the females' faces are dull brown. This coloration too is a possible avenue for female choice by Fisherian selection. One characteristic among primates has been clearly targeted for possible selection by Fisherian female choice—male penis size. Primate males living in groups with many females and many males, groups in which promiscuity is the mating rule, have long penes (Dixon 1978). Male chimps, in fact, use their penes for display toward estrous females. Because a longer penis would give a female pleasure (note that the human male has the longest and thickest penis of any primate), female choice might have been a factor driving penis length to extremes among primates. But examples such as these are few and far between, and no one has tested for the possibility of female choices in these specific examples.

In the second arena of female choice, primates should presumably

excel—smart and discriminating females making smart choices for their own reproductive benefit. Sometimes these “Triverian” choices can affect the evolution of male traits, but no matter, female choices affect females. And these smart primates, with the largest brains in the animal kingdom, should be putting their selective powers to work.

How Primate Females Choose

If female primates have been selected to make mate choices, how can they exercise those choices? Females can't count sperm, do health checks, or predict male vigor and then point at the chosen one. They can only make decisions based on cues provided by males and then try to make some attempt to gain a particular male. The task for the behaviorist looking for indications of female preference is to discover exactly how females express that desire, if and when it appears. They can't tell us, and we must rely on what they do to indicate favoritism or refusal.

It's sometimes impossible to tease out preference initiated by the female. We never know what's going on in her head or even whether she's thinking about an array of males at all. How would we know if she prefers male A over male B unless she makes a move toward him? It's much easier, however, to spot refusals, which are also an indication of female preference and choice. She can run away, sit down when an unwanted male approaches, or otherwise refuse to cooperate—the monkey version of having a headache. Japanese macaque females frequently refuse males who approach them in a very solicitous manner; the male cowers up to the female, bobs his head in her direction, lip-smacks, and then makes his intentions clear by turning his rear toward her (Enomoto 1974), but he's often foiled because the female isn't interested in him, or perhaps the timing just isn't right. As Michael Huffman reports for Japanese macaque females, “Regardless of the male's persistent attempts to initiate a mounting series, the females had control of the interaction” (1991b, p. 107). Huffman's view comes from observing that 43 percent of all copulation solicitations by males were refused by females. African vervet monkey females are just as uncooperative. Sandra Andelman reports that males were successful only 42 percent of the time they tried to have a sexual interaction with a female. Vervet females “sim-

ply sat down or walked away from males," she writes (1987, p. 788). Sometimes, when a male persisted, female refusal escalated into all-out attack on the pestering male. The irritated female would bite, chase, or hit a male; she might also solicit female allies and mob the so-called suitor. These refusals are sometimes the best indicators of female preference that we have—a nonchoice.

The act of positive preference can start with a close association. After all, females are most likely to copulate with males in the near vicinity. Just walking up to a male and staying near him will increase a female's chances of mating with him, but although a behaviorist may see "close proximity" as indicating favoritism it doesn't really prove preference, and certainly not choice in the evolutionary sense. A better indicator of a female's preference is the sexual present. A female walks up to a male, presents her hindquarters, and effectively "chooses" him for a mounting (see Figure 4). Presents of this nature are rarely given by females outside of estrus. During non-breeding season, the hindquarters' present means "I am of lower status than you and here I acknowledge it," and this submissive gesture is given most often to other females. But during estrus, the same present is a sexual invitation, and it's our clearest indication of a female preference. What could be more direct than having a female rear pushed into the male's face? The data on several kinds of non-human primates show that females are instrumental in initiating copulatory sequences by approaching males and sexually presenting. Barbary macaque females, for example, initiate most of the copulations in this manner (Small 1990b). This is also true of rhesus macaques, Japanese macaques, langurs, and many other species (Blaffer Hrdy 1977, Huffman 1991b, Manson 1991, Wolfe 1979).

Presenting her rear in the face of a male is not the only way a female shows her interest. A female might walk up to a male, quietly sit at his side or close to his back and grimace. She might make the interaction more intimate by a simple touch, or she'll reach out to groom him. A more motivated macaque female may leap on her favorite male and rub her genital area back and forth on the male's lower back (Wolfe 1979). A lion-tailed macaque female will pester a male over and over, especially if he ignores her. She'll rush past him, yank his tail or hair, or even jump up and down and screech. In captivity, frustrated lion-tails have been seen writhing on the floor in front of

a reluctant male (Lindburg, Shideler, and Fitch 1985). Female ruffed lemurs—black-and-white fluffy lemurs of the Malagasy forest—initiate copulations by approaching the male and slapping him (Foerg 1982). They might even beat him up to get his attention. On the other hand, if a male rudely tries to start a copulation without the female's first slap, he is beaten and chased away by the female. The same sort of female assertiveness occurs among capuchin monkeys in South America (Janson 1984). Females of this species chase the highest-ranking male, whine and whistle in his direction, and play a game of sexual tag. They run up, slap him lightly, and run away.

Even in species in which females seem overpowered by males, their subtle cues can influence what males get to do. Female *Hamadryas* baboons appear totally dominated by males (Kummer 1968), but females sometimes give nonconsort males subtle clues that let them know that the current partner is of no special importance. A nonconsort male will most often challenge an established consort and try to take possession of a female when he receives these sly clues from the female (Bachmann and Kummer 1980). Female *Hanuman* langurs are often terrorized by infanticidal males, yet the sequence of copulation is dictated by females. Langur females don't display any external signs of estrus—no swellings, no color changes. The only way a male langur knows a female is ready to mate is when she tells him so. The typical female langur in estrus walks up to a male, turns her back, crouches low, keeping her extra-long tail down, and bobs side to side in what primatologists call a "head shudder" (Blaffer Hrdy 1977, Sommer, Srivastava, and Borries in press). This dance of solicitation is repeated almost five times more often than responded to, and no one knows why males aren't always interested.

Females sometimes make their mate decisions under pressure. When a Japanese or rhesus macaque female sits next to a potential mate, she is often harassed by a higher-ranking male (Huffman 1987, Manson 1991). The unhappy male will run at the pair, and often attack the female; this is called a "consort intrusion." But the strategy seems useless for the attacking male. The pair almost always reunites, and interestingly enough, the female is always responsible for the reunion. Perhaps the low-ranking male is afraid to take the initiative after being attacked by one higher in status than himself. But even

in the rare cases when the female stays away from her former chosen partner, the victimizer doesn't have it easy. He still has to court her in the usual manner by approaches and inspections.

Females may also vie for a certain male. Although sexual selection theory suggests that males rather than females should be expected to fight over mates, limited access to especially preferred males can also result in female-female competition (Robinson 1982, Small 1988). Several times I've seen a Barbary female displace another female sitting next to a male. In almost all cases, a higher-ranking female quietly walks up close to the couple and the lower-ranking female moves away from the male. The female who interrupted didn't necessarily mate with the male, but she did stop any further interaction between her lower-ranking troop mate and the male. This policy is probably not that effective in Barbarys, however, because the displaced female could just move along to the next male.

And finally, a female might be able to affect a mate choice by altering sperm transport internally after copulation (Cohen and McNaughton 1974, Overstreet and Katz 1977). This suggestion seems quite wild, but as William Eberhard points out when writing about females and conception, "Female genitalia may be designed not only to facilitate fertilization, but also to prevent it under certain circumstances," (1990, p. 138). Eberhard suggests that the human female cervix moves away from the vagina during intercourse, almost as if it were blocking the way for sperm to enter the tiny hole. Also a certain amount of sperm spills out after copulation; consider the spillage when a human female stands up after intercourse. Postural change that causes spillage isn't exactly passive acceptance of male deposits. Although monkeys and apes aren't bipedal, they can and do sit upright. Sitting up may be a subtle attempt to empty the male's sperm out of her body. Also, if the female is mating with multiple males during her period of sexuality, the intromission by one male pushes aside the ejaculate of another male. Males of some species have responded to multiple deposits by evolving a semen that coagulates and forms a plug. This plug functions to keep sperm from falling out, but it can't stop another male from moving in. Once females move on to another male, the first suitor is virtually helpless if he can't physically stop her. It's then her decision.

We can also document the importance of female preference sometimes not by what females do but by what males do. Some primate males have courtship displays, although they are not all that common. Males perform this special pattern of behavior to attract females. The peacock's tail, and the way males use it, again, is the best example of a male display in a nonprimate. Primate males don't have such flamboyant options, but there's some evidence that males try. Their courtship displays are an indication of female power and confirmation that males don't run the mating game. For example, male chimps most often display to females in estrus to gain their attention (Goodall 1986, Tutin and McGinnis 1981). A male chimp doesn't just walk up and hop on a female. He patiently sits with his legs spread apart and waves his penis in her direction. He might also stare at her or shake branches at her. Because tension often runs high between male and female chimps, these displays tell a female that his interests are purely sexual in nature and that there's nothing to fear. Other primate males also resort to displays. When a mangleby male spots a female with a swelling, he tosses his heads rapidly back over one shoulder and the female often comes running (Wallis 1983). Japanese macaque males present their hindquarters to females. They sometimes attack females and threaten them as a sort of attention getter (Enomoto 1978, Huffman 1991b, Takahata 1982a)—not much of a way to court a female but certainly an instant avenue to her consciousness. In all these cases, it's the female who has the final say. Males in these species don't force females, but must win them over. The decision is up to the fairer sex.

Theory Meets Real Life

With all this theorizing comes more confusion than clarity. Female primates, like all animals, are supposed to be choosy. And when they make mate choices, they should attend to the quality of the male and make smart choices. If this is true, the behavior of female primates should support the theory. If not—and my observations of the Barbary macaques do not support the theory—there's something wrong with the theory, or at least it doesn't have universal application.

The task at hand, then, is to determine who conceives with whom and what role female actions play in the conception of offspring with particular males. To what extent can the mate preferences of female

primates be determined? How powerful are female primates in expressing their mating preferences? And do female preferences and choices have an evolutionary effect?

The next three chapters examine the reproductive physiology and sexual behavior of female primates, nonhuman and human, to show how theory meets real life, at least within the limitations of what we know about mating behavior today.