Monkeys and Men: Learning from Cayo Santiago [1]

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What does who opens the door on a date on a frigid Cambridge evening have to do with a lush island off the shores of Puerto Rico? For that matter, what does this island, teaming with squealing free-ranging rhesus monkeys, have to do with some of the best minds at Harvard?

I pondered these questions as I prepared to give a lecture on sexual selection theory to a group of Harvard students at the Puerto Rico Winter Institute this January. In a sense, the answer to the second question is easier to answer. Harvard scientist and prolific, two-times Pulitzer Prize winning author Edward O. Wilson reminded me last spring that his journey into what become the

field of sociobiology began on this island, known as Cayo Santiago, in 1956. Since then, Cayo Santiago has become a mecca for both scientists who study social behavior through observations of the social interactions and relationships of monkeys, and for evolutionary biologists of all sorts, who try to fathom the workings of the mind and language. Marc Hauser, Harvard psychologist and recent author of Moral Minds (Ecco Press), and his students have conducted ongoing research there for more than twenty years on Cayo Santiago.

Hauser works extensively in both the field and the laboratory. “What is exciting about working on Cayo Santiago is that you can ask profound questions about the evolution of mind to animals living in semi-natural conditions, and answer these questions with the rigor of captive experiments, and with the sample size of a drosophila geneticist,” observed Hauser recently.

So, going back to my first question, how does mundane dating etiquette connect to sexual selection and patterns of monkey behavior? Here is a quick tour of what I explained to the students.

Current divorce rates for the United States suggest that even if we manage to stay in a relationship there are always ups and downs. Many conflicts between men and women often arise from the differences between the sexes. How do we breathe, eat, or drink? We know how to satisfy these basic, primary needs. There are serious consequences for people who do not succeed at these tasks: they die. By contrast, if we do not find a mate, we only suffer, albeit a lot, if one is to judge by the plethora of self-help dating books for both men and women.

Our living primate relatives, such as monkeys and apes, can help us to recognize different reproductive decisions and strategies that continue to operate today. For those who do not succeed at reproducing, they die and with them go their genes. Natural selection favors those traits that lead to the greatest survival and reproductive success of the bearers. What is good for the goose is not necessarily good for the gander, and as we see in many animals, like humans, males and females often differ in behavior and appearance. Nearly 150 years ago, Charles Darwin began to unravel the selective forces driving these differences between the sexes.

Sexual Selection Theory

Darwin noted that some traits seemed to hinder survivorship. For example, the bright feathers of the male peacock are conspicuous to the female peahen. They also stick out like a sore thumb to predators, appearing as flags waving to predators, "eat me, eat me!”

To account for these sexually dimorphic traits Darwin developed the theory of sexual selection, a subset of natural selection. Sexual selection is selection for traits that enable individuals to acquire more and better mates. So while a trait may be damaging to survivorship it will be favored when it increases reproduction. Sexual selection occurs as a result of a character being non-randomly related to variance in reproductive success. As such, Darwin surmised that these gaudy feathers evolved because, while peacocks are clumsy in flight, the long fanciful tail is sexy to females and could enhance males' ability to reproduce.

Sexual selection theory provides a general framework from which we can explain communication differences between the sexes. This theory informs us that males are likely to compete against

one another for females, that females are the choosy sex, and that males advertise individual differences to attract females. While as a graduate student and before joining the faculty at Harvard, Robert Trivers explained in a seminal paper in 1972 why males do we they do and why females do something else. It is all about investment. This would be investment toward an offspring, in terms of time, energy, and risk at the expense of one's own fitness.

On Cayo Santiago, one can see first hand that female rhesus macaques are the investing sex, and this is typical for primates. Females get pregnant and once impregnated, females are required to carry the offspring to term. Women gestate for more than nine months, female rhesus do it for five and a half months, and both do it at a cost. Pregnancy is rather metabolically taxing. Pregnant females get hungry and lethargic. Imagine life as a pregnant rhesus monkey. You do not have supermarkets. You have to find your own food. This quest for food comes at the expense of doing other things, such as grooming and getting groomed, cultivating and maintaining social relationships, relaxing, or even taking care of your other kids. Once a mother, the investment expands. Infant rhesus require milk for at least the first 6 months of life, and a female cannot start cycling again immediately after birth, particularly if a mother is nursing on demand. It is very demanding keeping your eye on a playful infant, who could easily wander into the path of a competitor, or in the territory of a predator, if in the wild. Without the mother, the consequences can be quite devastating for an infant.

The extent to which a male invests varies across the primate order. Nevertheless, all in all, the extent to which the female primate invests in offspring care is far greater than any investment a male can devote to his offspring. A male's minimal investment is the sperm that he contributes.

It could certainly behoove a female to mate with a male who will stick around to help take care of her and their young. How is a female able to assess whether a male is able and likely to provide her or their offspring with direct benefits such as protection or even material benefits like food? Typically, socially dominant animals have priority of access to resources. When resources are in scarce supply it can greatly benefit a female to be connected to a male ally who can monopolize access to resources. Indeed, across many species there appears to be great evidence that females choose males on the basis of their dominance rank. Females also might exercise choice for males who can offer indirect benefits such as good genetic quality for her offspring.

Some of the research that has been done on Cayo Santiago helps us to understand some of those selection criteria. For example, evidence exists that female rhesus macaques prefer males that are socially novel to them and thus genetically different. This preference prevents inbreeding. Inbred offspring are typically less likely to survive and reproduce than outbred infants. Apart from checking out the new male on the block, females may also pay attention to individual differences between males in appearance to gain information about his underlying quality, or even how a male is likely to behave toward them.

Vervet Cheaters

There are all sorts of ways that men and women adjust themselves to make themselves more appealing. Women can wear make-up, and men can work out. Even playing hard to get is about sexual economics. By decreasing availability (not returning phone calls or playing "hard-to get"),

the value of that person goes up. Animals cannot cheat. They are what they are. I conducted some experiments in vervet monkeys, an African cousin to the rhesus monkey, to see what exactly happens when you help a male cheat. Male vervets exhibit varying intensities of blue and aquamarine color on their scrotum. Males who display resplendent colors tend to dominate their pale counterparts, so I painted pale males bright. I could not make an alpha out of a cheater, but brightly painted pale males tricked others, but not always in the faker's favor. While pale males acted nicely toward these imposters, brightly colored males perceived these males as a challenge and attacked, regardless of how the poor cheater behaved. Furthermore, females tended to act antagonistically toward these cheaters. Moral of the story: cheaters never prosper.

These studies of vervet monkeys underscore the importance of coloration in guiding social interactions between individuals in a captive setting. Vervet monkeys are not alone in spreading their words through color. Adult rhesus males and females exhibit reddened sexual skin (both faces and genitalia) during the mating season. While, color intensity increases throughout the mating season, it maxes out during the season's prime days of mating activity. Corri Waitt and colleagues wanted to determine whether females pay attention to this coloration in males. Their experimental study showed that females paid preferential attention to images of male faces that were digitally reddened over imaged of the same males who had paler faces.

As I reported to the students, the coloration a male rhesus monkey sports also directly affect their social interactions with others, even in the wild. In a more recent study I led on Cayo Santiago, we showed that males with greater face and genital hue spent more time associating with females in both nice, affiliative interactions and in sexual activities. Coloration does not appear to be threatening to females, as coloration was not associated with aggressive behavior, so we are surmising coloration is attractive to females for one reason or another.

At the Puerto Rico Winter Institute, I discussed with the students why females are the choosy sex, the possible criteria female primates use in their choice of mates and how females communicate interest in males and exercise mate choice. Although I highlighted these concepts by discussing patterns found in nonhuman primates, I informed the students that there is no typical primate, just as there is no typical human culture. The choices a female makes will be dependent on her environment, and social factors may constrain her preferences. Sexual selection theory can help us to understand human mating strategies and how men and women communicate. As we recognize common patterns among primate species we also see common threads among cultural groups of humans, which pronounce our common origins. By clarifying how sexual selection operates to affect male and female communication in primates, this may also shed light on some of the universal problems that plague humans such as: sex differences in crime, sexual jealousy, and why it is so difficult for humans to remain faithful.

Those are just a few of the things my research on Cayo Santiago has allowed me to understand and explore. And it will continue to provide an opportunity for Harvard and other researchers to learn about monkeys...and ourselves.

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