Primate Behavior: Sex and the Dominant Male

The concept of social dominance was first used in 1913 as a means to describe a pecking order among domestic fowl, and it quickly became an immensely popular element in the description of the social organizations of all sorts of animals, from vertebrates to invertebrates. Social dominance in primate groups, in particular, has been of great interest to ethologists, anthropologists, and psychologists, some of whom have managed to explain the outcome of nearly every kind of social interaction as an aspect of rankings in a dominance hierarchy.

Among the numerous hypotheses about the function of dominance hierarchies in primate groups, one of the most widely cited is that hierarchical rank is linked to reproductive success. This hypothesis and the very concept of social dominance are now being questioned by several investigators, who claim variously that dominance is unimportant to the social behavior of primates, that the definitions of dominance are incorrect, or that the social and physiological correlates of dominance remain to be determined.

The current emphasis in primatology on problem oriented, rather than descriptive, research has led investigators to reexamine how dominance is defined in order to determine whether it plays any of the roles ascribed to it. The problem of how to define dominance is a sticky one. Various definitions have been used and, in many cases, researchers have not explicitly stated how they determined dominance ranks in their studies.

According to Irwin Bernstein of the Yerkes Primate Research Center at Emory University, various measures of dominance do not agree with each other. Bernstein ranked captive monkeys in terms of mounting, grooming, and agonistic behavior (aggressive behavior and the responses to aggression). He concluded that these three proposed criteria of dominance are not consistent. Thelma Rowell of the University of California at Berkeley believes that many dominance hierarchies may exist only in the minds of the observers, who make primates compete in the laboratory for some reward, such as food, and then rank them with round-robin types of procedures. She stresses that social behavior evolved in free-living social groups and it is in such environments that dominance hierarchies should be studied.

In contrast to Bernstein and Rowell, Sandy Richards of Cambridge University reports that when captive rhesus monkeys are ranked according to other criteria, such as success in gaining access to food, as well as the criteria used by Bernstein, the various dominance rankings are in agreement. Since Richards' monkeys had to compete for access to food and drink and since the animals lived in groups consisting of one male, several females, and their offspring rather than the naturally occurring multimale groups, her results are subject to the criticism that she was not measuring dominance as it occurs when animals live in the wild.

The idea that sexual behavior is correlated with rankings in dominance hierarchies has led to the hypothesis that dominant males have greater reproductive success than their subordinates. Many investigators have reported evidence in support of this hypothesis. For example, Charles Southwick of Johns Hopkins University observed that dominant male rhesus monkeys in India apparently spend more time in consort with females and do more mounting than their subordinates. He interprets this to mean that dominance is probably associated with reproductive success.

The premise that observations of consortships and mountings can be used to measure reproductive success in rhesus monkeys is questioned by several investigators. For example, Lee Drickamer of Williams College found that high ranking male rhesus monkeys are more visible when they mate than lower ranking males, so observers may unintentionally bias their results unless they correct for this effect.

Susan Duvall of the University of Georgia, Bernstein, and Thomas Gordon of Emory University have recently completed biochemical tests of paternity of a group of rhesus monkeys at Yerkes to determine whether dominance ranks, which they measure by observing outcomes of agonistic interactions, are related to reproductive success. They conclude that no direct relation exists. Some low ranking, and even adolescent, males fathered as many offspring as the highest ranking males. Moreover, females have some choice in the matter of mating and they do not necessarily choose the highest ranking males.

Bernstein believes that female choice may have a great deal to do with male reproductive success and may even lead to a correlation between male rank and reproductive success. He bases this hypothesis on aspects of the social dynamics of groups of rhesus monkeys living on Caribbean islands off the coast of Puerto Rico that were reported by other investigators.

Donald Sade of Northwestern University determined that rhesus monkeys live in matriarchal societies. Females, he found, usually remain in the group they were born in and acquire dominance ranks equal to or just below those of their mothers. Males also inherit dominance ranks from their mothers. However, Stephen Vessey of Bowling Green State University and Drickamer report that 98 percent of young male rhesus monkeys leave the group they were born in before they reach maturity. By entering a new group, these males may improve their dominance ranks. Drickamer found that dominance ranks among males are correlated with age and seniority in the group.

Bernstein suggests that whether a male is well received by the females in a group determines whether he will stay with that group long enough to attain a high rank. If he stays with the group for a long time, he will father many of the offspring of that group. His rank may then be correlated with his reproductive success, but his rank would not be the cause of his reproductive success.

The relation between dominance rank and reproductive success among savanna baboons in Kenya was recently analyzed by Glenn Hausfater of the University of Virginia. Hausfater tested the hypothesis that dominant males, which were ranked by their agonistic behavior, will have a higher rate of copulation than subordinate males (the priority of access model) and that dominant males will father more offspring than subordinate males.

The priority of access model was first proposed in 1942 by C. R. Carpenter and was further developed in 1962 by Stuart Altmann of the University of Chicago. According to this model, dominant males have first access to females in estrus. Thus, if only one female in a group is in estrus at a given time, the first ranking male will mate with her. If two females are in estrus, the first and second ranking males will mate with them, and so on.

During 85 percent of the first 400 days that Hausfater observed the group of baboons, either one or no females were in estrus. Thus, according to the priority of access model, the vast majority of matings should involve the first ranking male. This expectation, however, was not fulfilled. Males other than the first ranking male had access to estrous females, but the baboons did not choose mates at random. For example, the two top ranking males (males changed ranks during the observation period) did not mate with three of the females even when no other females in the

group were in estrus. Hausfater believes it likely that the females chose the males rather than vice versa, but high ranking females did not necessarily mate with high ranking males. In fact, the three females that seemed to mate preferentially with the two top ranking males during the first 400 days of Hausfater's study had high, intermediate, and low ranks.

Although the priority of access model did not hold up, Hausfater did find that there was a relation between dominance rank and reproductive success in baboons. He believes, however, that this effect may not be significant over the lifetimes of the baboons. Apparently, high ranking males are most likely to mate with females on the days when the females are most likely to conceive. The males, though, change ranks often, so this result does not necessarily mean that any one male will achieve great reproductive success because of his dominance rank.

The stages of the ovarian cycle in a female baboon, and the days when conception is most likely to occur, are easy to detect because visible changes occur in the sexual skin of the female during her cycle. A female's sexual skin begins to swell a few days after the start of menstruation. The swelling reaches a maximum within 2 weeks and then the skin begins to deflate. Three days before the start of this deflation is the optimal time for conception to occur. (This is called cycle day D-3.) Females, though, can conceive on all days from D-1 to D-7.

Although the high ranking males were more likely to copulate with females on day D-3 of their cycle, Hausfater found that dominance rank alone could account for only about 56 percent of the variance in the proportions of copulations by the males. He suggests that males with different ranks may have different short-term reproductive strategies. Lower ranking males were more likely to consort with females on as many days between day D-1 and D-7 as possible, thus balancing the adverse effects of continually following a female and being harassed by other males with the possibility of impregnating the female on a day that is not optimal for conception. Dominant males, by consorting and mating with females on day D-3, maximize their chances of impregnating a female while they minimize the adverse effects of consortship.

Hausfater's hypothesis that the relation between dominance and mating behavior affects only short-term reproductive behavioral strategies of males hinges on two additional assumptions, neither of which has been proved or disproved: first, that each male, during the course of his reproductive life, spends equal amounts of time in each rank and, second, that no male is more likely than others to spend the most fertile period of his life in a high rank. If either of these assumptions does not hold, Hausfater believes it likely that different males may spend different amounts of time in each rank and thus use the short-term reproductive strategies to increase their reproductive success over the course of their lifetimes.

Like the rhesus monkey societies, societies of savanna baboons are matriarchal. Dominance ranks among female baboons are quite stable over long periods of time and a female inherits her rank from her mother. Males, on the other hand, change rank quite frequently.

During the first 400 days of his study, Hausfater observed no agonistically induced changes in female dominance ranks but saw one such change in male ranks occur every 21 days, on the average. He has recently analyzed data from 4 years of observations of the same baboon group that lead him to believe that males move freely through dominance ranks. Of the nine males that remained with the group during the 4 years, four were first ranking at some time. One of the two males that were first ranking during the first 400 days of the study later moved to rank 8 and the other moved to rank 4. Since no lifetime studies of dominance in baboons have been completed and since no evidence has been reported on the changes that occur in a male's fertility during the course of his lifetime, Hausfater's later results support his original hypothesis that dominance affects only short-term reproductive behavior, but are not conclusive. None of these recent quantitative analyses of the relation between dominance and reproductive success in rhesus monkeys and baboons confirm the idea that dominance is directly linked to reproductive success over the course of a male's lifetime.

Physiological Correlates of Dominance

Many investigators have begun to question the usefulness of the search for a behavioral function for dominance. Instead, they are beginning to look for physiological correlates of dominance. Bernstein, for example, points out that dominance hierarchies cannot be vital to primate social behavior since some primate groups have obvious hierarchies and others do not, yet all of the groups survive. It remains likely that when hierarchies are set up, the behavior of the group members is affected, but not in such a clear-cut way as by allowing dominant males priority of access to females.

According to Rowell, rigid hierarchies are often not normal features of primate social organization but may be behavioral manifestations of physiological responses to stress. When captured, certain species, such as macaques and baboons, set up hierarchies, but others, such as New World monkeys, do not. (Rowell speculates that if investigators had focused on New World monkeys rather than baboons and macaques, they would not be so obsessed with dominance.) Investigators have caused captive New World squirrel and capuchin monkeys to set up hierarchies, however, by reducing the amount of space available to them and by making the monkeys compete for food or to avoid shocks. Many monkeys living in the wild also apparently increase their agonistic interactions in response to stress. For example, urban rhesus monkeys, which must compete for scarce food, are far more aggressive than those that live in the forest. A captive urban monkey always dominates a captive monkey that had lived in the forest.

Rowell points out that low ranking, or submissive, monkeys have been found to exhibit physiological effects not felt by the more dominant animals. Submissive monkeys in caged groups, for example, overreact to injections of pituitary hormones and develop stress-related diseases, such as tuberculosis and ulcers.

Sade is also an advocate of studying physiological correlates of dominance and relating them to stress. He finds that differences in dominance ranks of female rhesus monkeys are related to differences in growth rates, ages of maturation, and ages when the monkeys first give birth to offspring. For example, Sade reports that most female rhesus monkeys first become pregnant when they are 3½ years old. However, a significant proportion of young females of high rank first become pregnant when they are 2½ years old. Drickamer finds, in addition, that more females of high rank than low give birth each year and that more of the offspring of high ranking females survive the first 12 months after their births. Sade believes that these physiological differences among females are not the result of genetic differences but are responses to different amounts of stress.

The new emphasis on physiological correlates of dominance is considered useful because, although physiology and behavior are interconnected, more than one kind of behavior can be associated with a physiological state. It now seems likely that no one kind of social behavior is correlated with dominance and that not all groups of primates even have dominance hierarchies. A focus on physiology, then, may provide one way to see what meaning dominance has in the lives of primates and what effect, if any, it has on rates of mortality and reproduction.—GINA BARI KOLATA