Experimental Field Studies of Asian Ape Social Systems

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The Asian apes, orangutans and gibbons, possess unusual social systems among anthropoid primates. Social groups of gibbons consist of mated adult pairs and their offspring; mature orangutans are primarily solitary. Recent experimental field research has begun to yield insights into the behavioral mechanisms employed by these animals to maintain their characteristic patterns of social dispersion. While spatial separation between female orangutans appears to be maintained passively, aggression, which is manifest during direct encounters and long-distance vocal interactions, mediates male asociality. Male–male aggression is the result of intense intrasexual competition occurring between animals for mating access to females. To reduce intrasexual competition, male orangutans have adopted alternative mating tactics. In contrast to female orangutans, female gibbons show marked agonistic tendencies toward conspecifics. Female territoriality contributes to preventing males from becoming polygynous. Male gibbons, restricted to monogamous relationships, attempt to ensure their paternity through intrasexual aggression. These observations suggest that the spatial dispersion of females constrains male mating options in both species. However, variations between orangutan and gibbon social systems can be understood as consequences of the temporal dispersion of sexually receptive females. The temporal clumping of females, due to relatively high operational sex ratios, limits the ability of male gibbons to acquire multiple mates. Conversely, an extremely low operational sex ratio in orangutans creates a strong selection pressure for

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introsexual competition and polygamous mating. These considerations provide a novel framework for interpreting the social systems of the African apes.

KEY WORDS: orangutans; gibbons; spacing; mating.

INTRODUCTION

The order primates is notable for the diversity of social systems displayed by different species. This diversity is especially apparent among our closest living relatives, the apes. Here social systems range in complexity from large, open unit-groups of chimpanzees and bonobos to mated pairs of gibbons and solitary orangutans (Tuttle, 1986). Attempting to account for the evolutionary origin and maintenance of this behavioral diversity is an appealing biological problem. For the past several years, I have conducted a program of field research investigating various aspects of the social systems of orangutans and gibbons. One goal of this research has been to evaluate the behavioral mechanisms used by individuals to maintain spacing and mating systems, which are two major components of animal societies.

While previous discussions have focused on ecological factors hypothesized to favor the evolution of ape social systems (Wrangham, 1979; van Schaik and van Hooff, 1983; Rodman, 1984), less attention has been paid to the actual behaviors used by these animals to mediate their characteristic patterns of social dispersion. Nevertheless, the structure of animal societies is a consequence of natural selection operating directly on the behavior of individuals, and a growing body of theory and empirical research suggests that an understanding of social systems depends on behavioral analyses that specify the relationships between animals (Rubenstein and Wrangham, 1986). These analyses stress the importance of examining the behavior of males and females separately.

Because of their greater investment in each zygote, females are a limiting resource for male reproduction in most species (Trivers, 1972). An inevitable result of this asymmetry in parental investment is that males and females differ in their reproductive behavior. While females will tend to act in ways that facilitate the conversion of environmental energy into offspring, male behavior will be characterized by attempts to achieve multiple matings. If female behavior ultimately constrains male mating options, variations in animal societies can be understood in terms of the interaction between female social dispersion and male mating tactics (Bradbury and Vehrencamp, 1977; Emlen and Oring, 1977; Wrangham, 1980). Consequently, recent analyses of animal social systems have begun with descriptions of female social relationships, and then have proceeded by examining how males interact with each other and with females.