SOCIAL STRESS AND THE SEX RATIO OF NEONATES AND INFANTS AMONG NON-HUMAN PRIMATES

by

C. P. VAN SCHAIK and M. A. VAN NOORDWIJK

(Laboratory of Comparative Physiology, State University of Utrecht, Jan van Galenstraat 40, 3572 LA Utrecht, The Netherlands)

SUMMARY

Recently, several theories have been put forward to account for deviations from unity in birth sex ratios among non-human primates. These theories propose benefits to the mother of adjusting the sex ratio of her offspring. Social stress has been suggested to provide the physiological mechanism for this adjustment. A review of sex ratios at birth and among infants in non-human primates indicates that high levels of social stress lead to both reduced female proportions at birth and increased female mortality after birth. In combination with behavioural observations showing that young females are more heavily attacked by conspecifics both before and after birth, these results suggest that the sex ratio adjustment is caused by the disruptive actions of conspecifics and is not the result of an adaptive adjustment by the mother. This implies that the theories proposed so far to explain this phenomenon are inadequate. A new hypothesis is presented, referred to as enforced density-dependent sex ratio change. It is adaptive for females to try to curtail the production of daughters by other females, because female fecundity in primate groups is negatively correlated with group size.

INTRODUCTION

Fisher (1958) argued theoretically that a female should invest equally in offspring of both sexes and showed that this could lead to deviations from a 1:1 sex ratio at birth because of sex-differences in pre-weaning mortality or in demands on maternal resources. According to this theory, the sex ratio at birth is fixed in a given population and all females should adhere to this optimum sex ratio (cf. Taylor & Sauer, 1980). Trivers & Willard (1973) were the first to point out that under certain circumstances it is adaptive for a female to deviate from this fixed sex ratio. Where the expected fitness of the sexes varies with external conditions or with maternal abilities, a female should produce the sex with the highest expected fitness. Since then, a number of hypotheses have been put forward to explain as adaptive variability in sex ratios at birth or afterwards among outbreeding organisms (Myers, 1978; Clark, 1978; Dittus, 1979; Maynard Smith, 1980; Altmann, 1980).

Among polygynous diurnal primates it has been found that high-ranking females give birth to relatively more daughters than low-
ranking ones in both wild (Altman, 1980) and captive (Silk et al., 1981; Simpson & Simpson, 1982) groups. This has been interpreted as adaptive for the females involved (Altman, 1980), because sons emigrate from their natal group by the time they reach sexual maturity (Packer, 1979), while daughters stay and generally attain ranks close to that of their mothers (Kawai, 1958; Hausfater et al., 1982). Given that female reproductive success is rank-dependent (Dunbar & Dunbar, 1977; Dittus, 1979), and assuming that the reproductive success of an emigrated male is not or only weakly correlated with his mother's rank, this leads us to predict the observed relationship. However, the rank-dependence in birth sex ratio is not always apparent, as can be ascertained from data presented by Koyama (1970), Breugemann (1978) and Grewal (1980). Moreover, the absence of a relationship is less likely to be perceived as striking and hence less likely to be reported (Clutton-Brock & Albon, 1982), so a systematic examination of the evidence and the design of critical tests are called for. As stressed by Simpson & Simpson (1982), acceptance of a theory on adaptive variation depends crucially on whether a proximate mechanism can be found that can produce this variation (cf. Williams, 1966). In this paper we will concentrate on the question of proximate causation.

Although sex ratios at conception have been found to be close to unity in the mammal species examined thus far, there are reasons to assume that differential fertilization by X- of Y-bearing sperm is possible (Clutton-Brock & Albon, 1982; but see Williams, 1979; Maynard Smith, 1980). Differential mortality of the sexes in utero is well documented (e.g. rhesus monkeys: Digiacomo & Shaughnessy, 1979), and seems to offer another possibility for the mother to manipulate the sex ratio. The problem lies not in a difficulty of conceiving direct mechanisms of sex ratio manipulation but in the physiological regulation of these mechanisms and their relation to external (social, ecological) conditions. Simpson & Simpson (1982) suggest that the timing of mating relative to ovulation provides a likely mechanism of adaptive sex ratio adjustment at conception in rhesus monkeys. However, the high copulation rates in the days surrounding ovulation in a great number of primate species and the fact that the survival of sperm is to be measured in days rather than hours (Thibault, 1973), render this suggestion at least not universally applicable. Altman (1980) suggested social stress as a plausible mechanism, since social stress tends to be rank-related in its physiological effects (Sassenrath, 1970). Simpson & Simpson (1982) rejected this possibility, because in their sample mothers receiving more aggression and showing more submission did not give birth to