

SEXUAL SELECTION, SEX RATIO AND MATING SYSTEM

That the total parental expenditure on male progeny must be equal to that on female progeny for maximal contribution to future generations has been well established by Fisher (1929, pp. 158-160) and Kolman (1960). While in theory this hypothesis can be applied to all sexually reproducing species, the following discussion deals only with those species in which some parental care occurs after fertilization.

Given a fixed amount of reproductive energy in a stable situation, there will be, on the average, an inverse relationship between the number of offspring produced and the energy expended on each individual offspring. Furthermore, let us assume that generally there is a direct relationship between energy expended per individual and the fitness of that individual. For each pair, then, the best reproductive strategy must be a compromise between the conflicting demands for production of the largest possible number of offspring and for production of offspring of the highest possible individual fitness. This will hold true for the total progeny as shown by Lack (1954, pp. 21-53) and also for the offspring of each sex considered separately.

Fisher has shown that the only way in which the primary sex ratio can be changed is by the alteration of the relative expenditure per individual of each sex. Emphasis has usually been placed upon events occurring during the period of parental care.

Sexual selection, however, takes the form of competition for mates in the period of independence from the parents and has sometimes resulted in the evolution of sexual dimorphism. If this dimorphism begins during the dependent period, and requires differential parental expenditure between the sexes, the compromise between number of offspring and their individual fitness will differ for males and females. In general, expression of color or pattern differences between the sexes seems to be postponed until the offspring have achieved independence, and therefore usually does not affect parental expenditure or the primary sex ratio. Size dimorphism, however, may begin to be expressed during the period of parental care (Williams, 1940; Ammann, 1938), and will usually necessitate differential parental expenditure on individual offspring of each sex except when concomitant dif-

ferential mortality equally influences expenditure in the opposite direction. With this exception, the primary sex ratio in size-dimorphic species may differ from that expected in nondimorphic species.

A positive correlation is also frequently found between size dimorphism and a polygamous or promiscuous mating system (Selander, 1958; Lack, 1940; Phillips, 1922-26). That the mating system is not necessarily the direct result of a skewed sex ratio is shown by the fact that sizeable populations of nonbreeding but sexually mature animals are known to occur. This has been shown for many birds (for example, Kessel, 1957; French, 1959; Orians, 1961; Fautin, 1941), and for some mammals (Bourliere, 1956, pp. 240-249). Furthermore, it has been observed that a male may acquire two females before his neighbor acquires even one (marsh wrens, Verner, in press; yellow-headed and red-winged blackbirds, Willson, personal observation), and that some male wrens may remain unmated for the season, while holding territories near males that become polygamous (Verner, in press; Armstrong, 1955). Armstrong and Verner found equal numbers of each sex, and males of both species are frequently polygamous. It is therefore unwise to conclude that adult or primary sex ratios necessarily determine the mating system of the species (see also Orians, 1961). Although there may be some cases in which adult sex ratio affects the mating system, the positive correlation between polygamy and the sex ratio can also occur because both are possible independent results of sexual selection.

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