

Extract from Trivers, Parental Investment & Sexual Selection (1972)

What governs the operation of sexual selection is the relative parental investment of the sexes in their offspring. Competition for mates usually characterizes males because males usually invest almost nothing in their offspring. Where male parental investment per offspring is comparable to female investment one would expect male and female reproductive success to vary in similar ways and for female choice to be no more discriminating than male choice (except as noted below). Where male parental investment strongly exceeds that of the female (regardless of which sex invests more in the sex cells) one would expect females to compete among themselves for males and for males to be selective about whom they accept as a mate.

Note that it may not be possible for an individual of one sex to invest in only part of the offspring of an individual of the opposite sex. When a male invests less per typical offspring than does a female but more than one-half what she invests (or vice-versa) then selection may not favor male competition to pair with more than one female, if the offspring of the second female cannot be parcelled out to more than one male. If the net reproductive success for a male investing in the offspring of one female is larger than that gained from investing in the offspring of two females, then the male will be selected to invest in the offspring of only one female. This argument is graphed in Figure 7.2 and may be important to understanding differential mortality in monogamous birds, as discussed below.

Fisher's (1958) sex ratio model compares the parental expenditure (un-defined) in male offspring with that in female offspring and suggests energy and time as measures of expenditure. Restatements of Fisher's model (for example, Kolman 1960, Willson & Pianka 1963, T. Ernlén 1968, Verner 1965, Leigh 1970) employ either the undefined term, parental expenditure, or the term energy investment. In either case the key concept is imprecise and the relevant one is parental investment, as denned above. Energy investment may often be a good approximation of parental investment, but it is clearly sometimes a poor one. An individual defending its brood from a predator may expend very little energy in the process but suffer a high chance of mortality; such behavior should be measured as a large investment, not a small one as suggested by the energy involved.

Parental Investment Patterns

Species can be classified according to the relative parental investment of the sexes in their young. In the vast majority of species, the male's only contribution to the survival of his offspring is his sex cells. In these species, female contribution clearly exceeds male and by a large ratio.

A male may invest in his offspring in several ways. He may provide his mate with food as in balloon flies (Kessel 1955) and some other insects (Engelmann 1970), some spiders, and some birds (for example, Calder 1967, Royama 1966, Stokes & Williams, 1971). He may find and defend a good place for the female to feed, lay eggs or raise young, as in many birds. He may build a nest to receive the eggs, as in some fish (for example, Morris 1952). He may help the female lay the eggs, as in some parasitic birds (Lack 1968). The male may also defend the female. He may brood the eggs, as in some birds, fish, frogs, and salamanders. He may help feed the young, protect them, provide opportunities for learning, and so on, as in wolves and many monogamous birds. Finally, he may provide an indirect

group benefit to the young (such as protection), as in many primates. All of these forms of male parental investment tend to decrease the disparity in investment between male and female resulting from the initial disparity in size of sex cells.

To test the importance of relative parental investment in controlling sexual selection one should search for species showing greater male than female parental investment (see Williams 1966, pp. 185-186). The best candidates include the Phalaropidae and the polyandrous bird species reviewed by Lack (1968). In these species, a female's parental investment ends when she lays her eggs; the male alone broods the eggs and cares for the young after hatching. No one has attempted to assess relative parental investment in these species, but they are striking in showing very high male parental investment correlating with strong sex role reversal: females tend to be more brightly colored, more aggressive and larger than the males, and tend to court them and fight over them. In the phalaropes there is no evidence that the females lay multiple broods (Hohn 1967, Johns 1969), but in some polyandrous species females apparently go from male to male laying successive broods (for example, Beebe 1925; see also Orians 1969). In these species the female may be limited by her ability to induce males to care for her broods, and female reproductive success may vary more than male. Likewise, high male parental investment in pipefish and seahorses (syngnathidae) correlates with female courtship and bright coloration (Fiedler 1954), and female reproductive success may be limited by male parental investment. Field data for other groups are so scanty that it is not possible to say whether there are any instances of sex role reversal among them, but available data for some dendrobatid frogs suggest at least the possibility. In these species, the male carries one or more young on his back for an unknown length of time (for example, Baton 1941). Females tend to be more brightly colored than males (rare in frogs) and in at least one species, *Dendrobates aurata*, several females have been seen pursuing, and possibly courting, single males (Dunn 1941). In this species the male carries only one young on his back, until the tadpole is quite large, but females have been found with as many as six large eggs inside, and it is possible that females compete with each other for the backs of males. There are other frog families that show male parental care, but even less is known of their social behavior.