

DEMOGRAPHIC ASPECTS OF THE SEXUAL SELECTION

Jiří Mlíkovský

*Laboratory of Evolutionary Biology, Czechoslovak Academy of Sciences,
Na Folimance 5, CS-120 00 Praha 2, Czechoslovakia*

ABSTRACT - A simple model is presented, describing how parental investment influences the sex ratio in natural populations. Possibilities of its further extension are briefly outlined.

KEY WORDS: Sexual Selection, Mating Systems, Parental Investment, Sex Ratio, Demography, Evolution

Since Charles Darwin's (1871) formulation of the concept of sexual selection, many efforts have been devoted to its study and the problem has been approached from most different aspects (for reviews see, e.g., Nikol'skij 1907, Nekrasov 1927, Huxley 1938, Maynard Smith 1958, Davitašvili 1961, Mayr 1972, Ghiselin 1974, O'Donald 1977, 1980, Otte 1979, Searcy 1982). It is, hence, not possible and not desired to repeat here the whole spectrum of problems included in the concept of sexual selection or closely connected with it. I will instead focus on one of those relevant problems which have been largely neglected in the study of sexual selection till now, namely on the demographic aspects of sexual selection.

The starting assumption of the model which is described further below is that the size of any species, i.e. the number of individuals which belong in it, is limited (1) by the carrying capacity of the particular niche which is inhabited by that particular species, and (2) by the body size of individuals belonging in it. This unequivocally follows from the fact that biomass turnover per time unit per space unit is independent of animal body size (Calder 1982) and that body size of organisms is optimized during evolution (Roff 1981, Ziojko and Kozjowski 1983; see also Calder 1983, Peters 1983, McMahon and Bonner 1983, and Schmidt-Nielsen 1984 for recent reviews of the ecological consequences of animal body size).

Whereas the above statements should presumably be valid for every species, what follows shall be for the sake of simplicity and clarity restricted to sexually reproducing animal species only, in which only two separate sexes and no sex reversals occur, and in which all individuals reproduce. The model shall be followed by a brief discussion of possibilities of its further extension.

Already Darwin (1871) hypothesized that the mating system should be closely related to the sex ratio. According to Darwin's (1871) prediction, sex ratio (defined as ratio of males to females) is 1 if mating system is monogamy, and it deviates from 1 in the case of polygamy, being smaller than 1 in the case of polygyny, and greater than 1 in the case of polyandry. This can be correct only if a number of hidden assumptions (*sensu* Blažek 1977, 1979) underlying the Darwin's hypothesis would be fulfilled in nature, what is apparently not the case (see below).

Turning now from these introductory remarks to the results proper, let us assume at first that both males and females contribute to their offspring only physiologically. Then, females are very important, while males function more or less only as triggers of reproduction. Note now that reproduction is a phenomenon which has a negative selective value for organisms (Williams 1966, 1975, Griffin 1983), but which serves as a mean of survival for populations, which are units of a higher level of organization than organisms (see, e.g., Kremjanskij 1969, Setrov 1971, Arnold and Fristrup 1982, Auger 1983). It is not surprising, hence, that populations which are particular forms of species existence in particular time (Mlíkovský and Zemek 1983) have survival strategies different from those of organisms*. They try to maximize their reparation ability, i.e. they try to be able at any time to produce as many individual organisms of which they consist as they have lost during the preceding time unit. Because the amount of their loss is basically unpredictable, populations have to try to consist of such organisms which will be able to maximally reproduce if necessary, i.e. they have to try to maximize the potential net reproductive rate of organisms (see Pianka 1978 for this term). In the extreme case, this strategy could lead to parthenogeny

*Note that in what follows I depart from the neo-Darwinistic reduction of evolutionary processes to the population level. For neo-Darwinists, goal of any individual (i.e. organism here) is to change the proportion of genes in a population in favour of its own genes. In this paper I consider the struggle for its own survival the goal of any biological system (at any level of organization).

(see Rostand 1950, Ivanova-Kazas 1970, 1977, and Cuellar 1977 for its distribution among animals), in which every organism may be considered a female, and in which no males are needed. It is probably for genetic reasons that this extreme strategy is not favoured in evolution (Maynard Smith 1971a, b, 1978, Williams, Mitton 1975, Felsenstein 1974, 1985, Stanley 1975, Williams 1975, Bell 1982, Lange 1982, Griffin 1983, Panfil 1984, Bernstein et al. 1984, 1985, Gläser 1985, Penny 1985)*.

Hence, a minimum number of males is needed in any population with a good evolutionary perspective. But if we still assume that males function only as triggers of reproduction, the sex ratio would still approach zero. However, the situation changes markedly if we recognize that if males invest in their progeny more than but their sperm cell, the net reproductive rate may be increased. Hence the function

$$I_m = f_1(R_0) \quad (1)$$

where I_m is parental investment of male, and R_0 is net reproductive rate, is monotonously increasing towards an asymptote. The increase of parental investment** causes, however, that males are able to trigger fewer females to produce progeny than previously and, because the size of any particular population is limited as stated above, it follows from this that the sex ratio changes (increases). Hence, the function

$$I_m = f_2(SR) \quad (2)$$

where SR is sex ratio (males to females), is monotonously increasing. Because further

*Population geneticists suggest in this respect usually that the optimal sex ratio at the age of reproduction is 1:1, but that it can vary under certain conditions (e.g., Fisher 1930, Crew 1937, Shaw and Mohler 1953, Shaw 1958, Kolman 1960, Edwards 1962, Vermer 1965, Crow and Kimura 1970, Spieth 1974, Eshel 1975, Maynard Smith 1978, Uyenoyama and Bengtsson 1979, Williams 1979, Green 1980). Just like Darwin's (1971) original hypothesis, this may be true only if a number of hidden assumptions underlying these hypotheses would be fulfilled in nature, what is usually not the case. A closer analysis of them would, however, go beyond the frame of this paper.

**I follow here and in the following text Triver's (1972) terminology, which is now more common and more elaborate than the original terminology proposed by Fisher (1930).

$$SR = L_m/L_f \quad (3)$$

where L_m and L_f are proportions of adult males and females, respectively, in a population, it follows from the equation (2) that

$$I_m = f_4(L_f) \quad (4)$$

and that the latter function (4) is monotonously decreasing.

Because the whole offspring production in a population is, per definitionem, proportional to the product of R_0 and L_f , and, as stated above, this number will be maximized by any population, it follows from the equations (1) and (4) that

$$SR = f_5(R_0 L_f) \quad (5)$$

and that this is an optimal function. The exact position of the turning point of this function will naturally vary and will be dependent on particular life history parameters in any particular population and in any particular situation.

In what follows, I shall briefly outline some few possibilities of the extension of the very simple model presented here. Listed are naturally occurring deviations from the assumptions underlying the above model and mentioned above in this paper.

(1) Reproductive value and ability to parental investment change markedly with age in both males and females (cf., e.g., Comfort 1964, Emlen 1970, 1973, Caswell 1982, 1984).

(2) Only a certain part of males and females in reproductive age is actually involved in reproduction, their sex ratio being known as the operational sex ratio (Emlen and Oring 1977). The other part is usually called floating population. Its existence has been proved in several field experiments with birds and mammals (see Krebs and Woldendorp 1981). The proportion of the floating population can be rather large; e.g., for various waterfowl species (Aves: Anseridae) I calculated a value of about 38% (Mlíkovský, unpubl. data).

(3) Within a species, different mating systems can occur at the same time, and there are more mating systems known than simply monogamy and polygamy (Orrians 1969, Emlen and Oring 1977, Wittenberger 1979, Oring 1982, Panov 1983).

(4) Reproductive value and ability to invest into the progeny may well differ from each other in any particular individual. For example, females with the reproductive value zero, i.e., e.g., females in the post-reproductive age, may still invest very much in their grandchildren in the role of grandmothers.

(5) More than two sexes can occur in a single species. This condition was described in various protists, where the individual sexes were called syngens by Sonneborn (see Sonneborn 1957, Génermont 1985).

(6) Other types of sexuality than simple bisexuality exist in nature, e.g. hermaphroditism (Smith 1967, 1975, Ghiselin 1969).

(7) Socially induced sex reversals are possible in various species, e.g. in many fish species (Chan 1977, Chan and Yeung 1983).

(8) The so-called helpers can occur in a population (Skutch 1961, Brown 1978, Oring 1982).

(9) The so-called casts of workers can occur in various species, e.g. in many social insects, which do not reproduce, but only invest in the offspring of individuals belonging to other casts (cf. Wilson 1971).

(10) Various genetic effects can alter sex ratio (see Hohenboken 1981, and Robinson 1983 for reviews).

Without any doubt, several more complications of the model outlined in this paper could be listed here, but I see no reason in doing so at moment. It should be the matter of future work to discover and to investigate them, and to incorporate them subsequently in the simple model presented here. I believe that this will be valuable for both ethology and ecology and, moreover, that it will help to promote the co-operation of ethologists and ecologists in areas of interest common to both of them.

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