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A New Theory of Sexual Investment

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Summary. It is argued that an appropriate model for the evolution of sexual investment, at least in higher vertebrates, may be as follows. The primary sex ratio is fixed at unity, parents can recognise the sex of individual offspring, and the returns (in offspring fitness) are different for the two sexes. For this model, it is shown that it is evolutionarily stable to invest differently in sons and daughters. In particular:

i) If for a given investment the probability of survival is lower for one sex, selection favours greater investment in that sex.

ii) If one sex has a frequency-dependent component of fitness, such that individuals receiving a greater-than-average investment are fitter, selection favours greater investment in that sex.

iii) If the sex of an offspring can be recognised after an investment d, it may be evolutionarily stable to invest only in some fraction r of the more expensive sex, and to abandon a fraction $(1-r)$. However, such behaviour can evolve only if d is a small fraction of the total investment required per offspring.

Introduction

Since the time of Fisher (1930), the problem of the evolution of the sex ratio has been formulated as follows. It is supposed that the sex ratio is an evolutionary variable under genetic control, usually by genes expressed in a parent, but that there is some fixed and unvarying cost of sons and daughters. These assumptions may often be inappropriate. On the one hand, there is remarkably little evidence for genetic variance of the sex ratio, except in haplodiploids. The data are briefly reviewed in Maynard Smith (1978). The most striking observations are, first, that there is no evidence of genetic variance of the sex ratio in man, despite massive amounts of data, and second, that the sex ratio of domestic poultry and cattle remains obstinately at unity despite the great economic advantages of a female bias. There are some clear examples of genetic variance (e.g. Weir 1962), but they are few and far between.

In contrast, it seems quite possible, at least in higher vertebrates, that parents might be able to recognise the sex of their offspring, and to invest differently in them according to sex. The problem addressed in this paper is therefore as follows. Suppose that the primary sex ratio in some species is fixed at unity. Suppose also that parents can recognise the sex of their offspring, and that the fitness (survival and/or breeding success) of those offspring varies differently with parental investment for the two sexes. Will parents evolve so as to invest differently in sons and daughters, and if so to what extent?

The Model

It is supposed that an individual female invests m in each son and f in each daughter, and produces a total of n sons and n daughters, subject to the constraint

$$n(m+f)=C, \tag{1}$$

where C is the total investment available. Fathers do not invest in their offspring (or all fathers invest equally).

Suppose that typical members of the population invest m^* in each son, and that a rare mutant type of female invests m in each son. The fitness of a son receiving investment m will depend both on m and m^*, and will be written $\psi(m, m^*)$. It will also depend on the investment being made in females, because, with a sex ratio of unity, the mean fitness of males and females must be equal. Thus $\psi(m, m^*)$ is the

Table 1

Mating		Frequency	Daughters		Sons	
♀	♂		*Aa*	*aa*	*Aa*	*aa*
Aa	*aa*	P_1	$\frac{1}{2}\frac{C}{(m^*+f)}\phi(f)$	$\frac{1}{2}\frac{C}{(m^*+f)}\phi(f)$	$\frac{1}{2}\frac{C}{(m^*+f)}\psi(m^*)$	$\frac{1}{2}\frac{C}{(m^*+f)}\psi(m^*)$
aa	*Aa*	P_2	$\frac{1}{2}\frac{C}{(m^*+f^*)}\phi(f^*)$	$\frac{1}{2}\frac{C}{(m^*+f^*)}\phi(f^*)$	$\frac{1}{2}\frac{C}{(m^*+f^*)}\psi(m^*)$	$\frac{1}{2}\frac{C}{(m^*+f^*)}\psi(m^*)$
aa	*aa*	$1-P_1-P_2$	–	$\frac{C}{(m^*+f^*)}\phi(f^*)$	–	$\frac{C}{(m^*+f^*)}\psi(m^*)$

fitness of a male receiving investment m (in a population in which typical males receive investment m^*) relative to the fitness $\psi(m',m^*)$ of a male receiving investment m'. The differences in absolute fitness of males which arise because of differences in the numbers of females present are not allowed for in ψ. The corresponding expression for the fitness of females is $\phi(f,f^*)$.

An example may help to make these expression for male and female fitness clearer. Suppose first that the probability that a male surviving to become an adult is $\alpha(m)$, and of a female surviving to become an adult is $\beta(f)$; that is, these survival probabilities depend only on investment in the individual, and not on average investment. Suppose further that all adult females have equal expectations of breeding success, but that the breeding success of a male depends on the difference between the investment it receives and the average investment. Then $\phi(f,f^*)=\beta(f)$ and $\psi(m,m^*)=\alpha(m)\gamma(m-m^*)$. Finally, if m^* and f^* are such that $\alpha(m^*)=2\beta(f^*)$, there will be twice as many adult males as adult females, so each male can expect only half as many offspring. This last effect is not included in ϕ and ψ but is allowed for in the way the recurrence equations are set up. It will be convenient to write the fitness functions as $\phi(f)$ and $\psi(m)$, but their full form must be remembered when interpreting the results.

Let the evolutionarily stable state of a population be m^*, f^*; that is, typical mothers invest m^* and f^* in sons and daughters respectively. Consider the fate of a rare mutant A such that Aa females invest m^* in each son and f in each daughter. In one generation let the frequencies of Aa ♀ × aa ♂ and aa ♀ × Aa ♂ matings be P_1 and P_2 respectively. If mating is random, we can ignore AA genotypes and $Aa \times Aa$ matings.

Table 1 shows the number of offspring, weighted by their fitnesses. Hence, if P_1' and P_2' are the corresponding frequencies in the next generation,

$$\left.\begin{aligned} P_1' &= \frac{1}{2}\frac{m^*+f^*}{m^*+f}\frac{\phi(f)}{\phi(f^*)}P_1+\frac{1}{2}P_2 \\ P_2' &= \frac{1}{2}\frac{m^*+f^*}{m^*+f}P_1+\frac{1}{2}P_2 \end{aligned}\right\} \tag{2}$$

Hence $P_1'+P_2'=RP_1+P_2$, where

$$R=\frac{1}{2}\frac{m^*+f^*}{m^*+f}\left[1+\frac{\phi(f)}{\phi(f^*)}\right]. \tag{3}$$

If $f=f^*$, then $R=1$ (as is obvious, if the mutant is identical to the rest of the population). If m^*, f^* is to be proof against invasion by any mutant f, then $R<1$ if $f \neq f^*$. Hence, provided R is a differentiable function,

$$\left(\frac{\partial R}{\partial f}\right)_* = 0, \tag{4}$$

and

$$\left(\frac{\partial^2 R}{\partial f^2}\right)_* < 0. \tag{5}$$

Substituting for R in (4) gives

$$(m^*+f^*)\frac{\phi'(f^*)}{\phi(f^*)}=2. \tag{6}$$

By an exactly similar argument, considering a mutant investing m in males and f^* in females,

$$(m^*+f^*)\frac{\psi'(m^*)}{\psi(m^*)}=2. \tag{7}$$

From (6) and (7),

$$\frac{\phi'(f^*)}{\phi(f^*)}=\frac{\psi'(m^*)}{\psi(m^*)}. \tag{8}$$

This can be expressed in words by saying that, at an ESS, the percentage increase in fitness of females resulting from additional investment equals the percentage loss of fitness of males resulting from the loss of that same investment. It is a special case of Charnov's (1979) assertion that "Selection favours a mutant gene which alters various life history parameters iff the % gain of fitness through one sex function exceeds the % loss through the other sex function."

The stability of the equilibrium depends on (5). Using (6), this can be reduced to the condition $\phi''(f^*)<0$; there is of course the corresponding requirement that $(\partial^2 R/\partial m^2)_* < 0$, which reduces to $\psi''(m^*)<0$. Unfortunately, these conditions can only be checked by solving Eqs. (6) and (7) for f^* and m^*. I have examined some numerical examples of the equilibria discussed below, and found them to be stable, but I am unable to provide any general proof of stability.

To obtain a more practical feel for what is implied by Eqs. (6)–(8), I now consider some special cases. First, suppose the fitness functions are different for the two sexes, but not frequency-dependent; that is, ϕ depends on f but not f^* and ψ on m but not on m^*. For example suppose

$$\phi(f)=f^a/(1+f^a); \qquad \psi(m)=m^a/(b+m^a).$$

Then $\phi'(f)/\phi(f)=a/(1+f^a)f$,

$\psi'(m)/\psi(m)=ab/(b+m^a)m$,

and hence from (8)

$$bf^*(1+f^{*a})=m^*(b+m^{*a}). \tag{9}$$

If $b>1$, then for a given investment females are more likely to survive than males, and it follows from (9) that $m^*>f^*$. (This inequality can be seen as follows. For $m=f$, LHS>RHS. Also, $d(\text{LHS})/df>0$ and $d(\text{RHS})/dm>0$. Hence, if LHS = RHS, $m^*>f^*$.)

Hence if for a given investment females are more likely to survive than males, at an ESS more will be invested in males. However, although this will usually be the case, it is possible to find functions relating fitness to investment for which the statement does not hold.

Now consider the case in which both sexes have the same non-frequency-dependent probability of survival, $\phi(f)$ and $\phi(m)$, as a function of investment, but one sex (e.g. the male) has an additional fitness component according to whether it receives more or less than the average investment. That is

$$\psi(m)=\phi(m)[1+\theta(m-m^*)], \tag{10}$$

where $\theta(0)=0$, and $\theta'(0)>0$, implying that a male receiving a greater than average investment is fitter than average. Combining (8) and (10) gives

$$\frac{\phi'(m^*)}{\phi(m^*)}+\theta'(0)=\frac{\phi'(f^*)}{\phi(f^*)}. \tag{11}$$

For most plausible functions, $\phi'(m)/\phi(m)$ decreases monotonically with m; this is so, for example, if $\phi(m)=m^a/(b+m^a)$ with a and b positive. In this case, $m^*>f^*$. Hence, if one sex has an additional frequency-dependent component of fitness, investment in that sex will be greater.

So far, I have supposed that a parent makes the same investment in all offspring of a given sex. However, it might pay to invest heavily in some individuals and little in others. In the extreme case, suppose that the sex of an offspring is known to the parent before any investment has been made. By not investing at all in some offspring, the parent can in effect determine the sex ratio among its offspring. Then, from Fisher's (1930) argument, we expect the total investment in males and females to be equal.

More generally, suppose there is a minimum investment d in each offspring before the sex of that offspring is known to the parent. A female produces n offspring of each sex, and raises all her daughters and a fraction r of her sons. Then the constraint equation becomes

$$nrm+n(1-r)d+nf=C.$$

Now suppose that typical aa females have the phenotype m^*, r^*, f^* and that rare mutant Aa females have the phenotype m^*, r, f^*. Equations (2) then become

$$P_1'=\frac{1}{2}\frac{d+r^*(m^*-d)+f^*}{d+r(m^*-d)+f^*}P_1+\frac{1}{2}P_2,$$

$$P_2'=\frac{1}{2}\frac{r[d+r^*(m^*-d)+f^*]}{r^*[d+r(m^*-d)+f^*]}P_1+\frac{1}{2}P_2.$$

Then $P_1'+P_2'=RP_1+P_2$,

where $R=\dfrac{1}{2}\dfrac{(r+r^*)[d+r^*(m^*-d)+f^*]}{r^*[d+r(m^*-d)+f^*]}$.

The equilibrium condition $(\partial R/\partial r)_*=0$ gives

$$r^*=\frac{f^*+d}{m^*-d}. \tag{12}$$

When $d=0$ (i.e. offspring sex can be recognised before any expenditure), $r^*m^*=f^*$. That is, total expenditure on the two sexes is equal.

If $(f^*+d)/(m^*-d)>1$, then the ESS is to invest m^* in all sons and f^* in all daughters, where m^* and f^* are given by Eqs. (6) and (7).

If $(f^*+d)/(m^*-d)<1$, then it is no longer evolutionarily stable to invest in all sons. Instead, investment in some males should cease at d. If $r^* \neq 1$, then Eqs. (6) and (7) must be replaced by

$$[r^*(m^*-d)+d+f^*]\frac{\phi'(f^*)}{\phi(f^*)}=2, \tag{13}$$

and

$$[r^*(m^*-d)+d+f^*]\frac{\psi'(m^*)}{\psi(m^*)}=2r^*. \tag{14}$$

Fortunately, (12) can be used to eliminate r^* and m^* from (13), and r^* and f^* from (14), to give

$$(f^*+d)\frac{\phi'(f^*)}{\phi(f^*)}=1, \tag{15}$$

$$(m^*-d)\frac{\psi'(m^*)}{\psi(m^*)}=1. \tag{16}$$

For given ϕ and ψ, Eqs. (15) and (16) can be solved for f^* and m^*, and Eq. (12) then gives r^*.

To take a particular case, let $\phi(f)=f^2/(1+f^2)$ and $\psi(m)=m^2/(2+m^2)$. Then with $d=0.02$, $f^*=1.01$, $m^*=1.174$ and $r^*=0.90$. Hence 10% of sons are not raised. However, with $d=0.10$, $r^*>1$; in other words, all sons are raised. Thus, as expected, if the minimum investment d is low enough, it is evolutionarily stable not to raise some of the more expensive sex. However, the numerical example suggests that d must be a very small fraction of m^* before this is an evolutionarily stable option.

These conclusions have been stated for the case in which for a given investment the fitness of sons is lower than that of daughters. If daughters require more investment than sons for a given fitness, then it may be stable for only some daughters to be raised beyond d.

Throughout the analysis, I have supposed that the level of investment is determined by the mother. Identical conclusions follow if it is determined by the father.

Discussion

If the primary sex ratio is unity, but the fitness of sons and daughters depends differently on parental investment, it will in general be evolutionarily stable to invest differently in the two sexes. In particular

i) If, for a given investment, the (non-frequency-dependent) probability of survival of males is greater than of females, the ESS is to invest more in females, and vice versa.

ii) If the probabilities of survival of the two sexes are equal, but one sex has an additional frequency-dependent component of fitness, such that individuals receiving a greater than average investment are fitter, then the ESS is to invest more in that sex.

iii) If the sex of offspring can be recognised by their parents after some investment d, then it may be evolutionarily stable to invest further only in some fraction r of the more expensive sex, and to abandon a fraction $1-r$ after an investment d. However, a numerical example suggests that d must be a very small fraction of total investment in an individual before this option will be favoured.

Are there any data which bear on these predictions? In fact, the theoretical investigation was stimulated by two sets of data. The first (Clutton-Brock et al., to be published) concerns the red deer, *Cervus elephas*. This is a polygynous species, in which the success of a male in holding a harem depends on body weight and condition. The variance of male reproductive success is greater than of females. There is no evidence for adaptive variation of the sex ratio. Females do invest more in sons than daughters early in life. Duration of gestation and birth weight is greater for male calves. Males suckle more often and grow faster. Hinds which have reared a male calf in the previous season are nearly twice as likely to fail to produce a calf in the following year, apparently because they fail to conceive. Those which do conceive after rearing a male do so later.

These data fit well with prediction (ii) above. There is evidence for frequency-dependent fitness in males, and of greater investment in them. However, as the authors point out, there is an alternative explanation. Female offspring remain in the same area as their mothers and compete with them for food, whereas males disperse. Therefore, although maternal investment is often greater in sons during the first two years, this may be counterbalanced by greater investment in daughters later on. This resembles the explanation by Clark (1978) of the male-biassed sex ratio in Galagos, although she proposes that daughters compete with each other rather than with their mothers. This in turn resembles Hamilton's (1967) explanation of female-biassed sex ratios arising because of local mate competition. The data do not enable us to distinguish between these hypotheses.

The second data set was that of Dittus (1979) on the Toque monkey, *Macaca s. sinica*. Infant and juvenile mortality is substantially higher in females than males; this results mainly from behavioural interactions which limit access to food. Male mortality is higher in young adults at the time of dispersal. There is no evidence that the variance of reproductive success is greater in males, but it probably is so. Nor is it clear that the higher female mortality can properly be assigned to a lack of 'parental investment'. The picture is therefore less clear than in the red deer. An alternative explanation is again possible, since females remain in the troop and continue to compete with their mothers and sisters, whereas males disperse.

I know of no data to suggest that some fraction of the more expensive sex is abandoned early in life (prediction iii). This is a selectively favoured option only if recognition is very early. In mammals it would imply recognition before birth and selective resorbtion or abortion; in birds it would imply recognition at or soon after hatching.

If differential parental investment is observed, the main problem is to distinguish between the hypothesis proposed here, and the hypothesis that offspring are competing for resources with their parents or each other. Ideally, we need to examine polygynous species in which either there is no sex difference in dispersal, or in which females disperse more.

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References

Charnov EL (1979) The genetical evolution of patterns of sexuality: Darwinian fitness. Am Nat 113:465–480
Clark AB (1978) Sex ratio and local resource competition in a prosimian primate. Science 201:163–165
Clutton-Brock TE, Guinness FE, Albon SD (to be published) Parental investment in male and female offspring in a polygamous mammal.
Dittus WPJ (1979) The evolution of behaviour regulating density and age-specific sex ratios in a primate population. Behaviour 69:265–302
Fisher RA (1930) The genetical theory of natural selection. Oxford University Press, Oxford
Hamilton WD (1967) Extraordinary sex ratios. Science 156:477–488
Maynard Smith J (1978) The evolution of sex. Cambridge University Press, Cambridge
Weir JA (1962) Hereditary and environmental influences on the sex ratio of PHH and PHL mice. Genetics 47:881–897