

Why do females care more than males?

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SUMMARY

Females tend to provide more parental care than males. Previous efforts to account for this have been confused because it is difficult to express the costs of care for males and females in the same currency. Here I propose a null model that does so, using the Fisherian constraint that total male and female reproduction must be equal. The model shows that, contrary to a number of recent analyses, lower probability of parentage for males does tend to make males less likely than females to provide care. It also shows how sexual selection stemming from pre-mating asymmetries in investment promotes similar post-mating asymmetries.

1. INTRODUCTION

One of the primary rules of thumb of animal social behaviour is that females tend to be the caring sex, while males focus more on mating (Bateman 1948; Trivers 1972; Clutton-Brock 1991). Part of the explanation lies in the gamete dimorphism that defines the sexes; prior to mating one sex specializes on nourishment and the other on motility (Parker *et al.* 1972; Alexander & Borgia 1979). But after mating, when either parent could provide further care, female care still tends to predominate (Clutton-Brock 1991). It is clearly tempting to try to explain post-mating asymmetries in parental care from the pre-mating asymmetries, but this has proven difficult. I suggest that part of the problem is that we have left a fundamental constraint out of the analysis. Including it transforms the arguments and clarifies two ways in which selection tends to promote care by females rather than males.

The constraint is well known; each offspring has a mother and a father, so all males reproduce the same amount as all females. Fisher (1930) used this principle, and its corollary that individual males and females reproduce equally when they are equally numerous, to explain the evolution of the sex ratio.

Beginning from a state of no post-mating care, which sex will first meet the conditions selecting for care, assuming only the asymmetries of pre-mating investment? What we need is a null model for what to expect in the absence of any idiosyncratic factors. Assume that males and females are, on average, equally adept at caring. Either could provide same benefit, b , to the offspring. Assume also that providing such care is also equally costly for each; it involves the same amount of risk, the same expenditure of time, or the same physiological drain. The difficulty lies in comparing costs, because caring females and males may forego such different things. For example, females might put resources into fewer future eggs, while males

would suffer in competition for mates, so how do we compare? The key is to remember that the total reproduction of each sex is equal; let's call it x . If m and f are the numbers of males and females, the average male reproduces x/m and the average female x/f . The most obvious meaning of equal cost of care is that it costs an average male and an average female the same fraction, c , of their expected success. So the costs can be set as cx/m and cx/f for the average male and female, respectively.

This way of expressing the costs is not an inexorable law of nature. Various factors could cause the same physiological cost to map differently to fitness for males and females. But it has two advantages. First, it expresses the costs in a common currency, making explicit the constraint that total male reproduction equals total female reproduction. Second, it expresses a reasonable null model for comparing the costs of an action to males and to females even when they strive for fitness in very different ways. It expresses the idea that, in the absence of special factors, a given physiological cost should have a similar effect on whatever a male is trying to do as it does on whatever a female is trying to do.

Under an equal adult sex ratio, the argument so far predicts no bias towards female care. Benefits and costs are the same for males and females. The obvious further implication is that, if one sex is consistently rarer, its cost will be larger so it will be less likely to be parental. But there are two additional implications that are more interesting, one concerning the importance of parentage and the other about the role of sexual selection.

2. PARENTAGE AND RELATEDNESS

This framework can help resolve the issue of whether the probability of parentage affects which sex will

provide care. Trivers (1972) argued that when a female's brood is sired by multiple males, each male has lower expected relatedness to the brood, making him less likely than the female to provide care. Others (Maynard Smith 1978; Grafen 1980; Werren *et al.* 1980; Westneat & Sherman 1993) have disagreed, noting that a male who eschews care to seek other mates will, on average, have no higher paternity in his future matings, so that paternity factors out of the male care equation (though it may remain in some form when paternity can be expected to differ between the two sets of offspring; Werren *et al.* 1980; Westneat & Sherman 1993). The view that parentage does not necessarily matter seems to have been generally accepted, though it has been recognized that the question of male versus female care may be more complicated than the single-sex analyses in which paternity cancels out (Maynard Smith 1978; Clutton-Brock 1991; Westneat & Sherman 1993). In contrast, Trivers (1985) has continued to assert that paternity does matter. The model developed here supports Trivers's view.

Suppose, for the average mated pair, parentage to their brood differs. The female is the mother of all the offspring, while the male is the father of only a fraction p , owing to multiple mating by his mate. The benefit a male gives to his own offspring in the current brood is therefore pb . Using the benefit-cost model above, males and females are selected to provide care when:

$$pb > \frac{cx}{m} \quad (1)$$

$$b > \frac{cx}{f} \quad (2)$$

The left-hand sides are for benefits to current true offspring, and the right-hand sides are for costs in terms of future offspring. Both sides could be multiplied by 0.5, for relatedness to true offspring, without affecting the results. Clearly, when the sex ratio is unity ($m = f$), the female condition is easier to meet. The genetic costs are the same, but the male would obtain a smaller genetic benefit by providing care because of his lower parentage to the current brood.

Note that paternity has been assigned as p in the benefit term for males, but not in the cost term. This is correct, because p is necessary on the left-hand side to obtain the benefit to male's number of true offspring in the brood, while c on the right-hand side is already defined in terms of true offspring (defined as all the offspring the male could have sired if he did not provide care, including any from promiscuous matings). But what of the argument noted above (Maynard Smith 1978; Grafen 1980; Werren *et al.* 1980; Westneat & Sherman 1993) that males with low paternity will also have lower paternity in their future broods? It is possible to make p disappear from inequality (1) by redefining the costs in terms of broods, but this requires a linked change in inequality (2), leaving the male-female comparison unchanged. Let C be the fraction of future broods (rather than true offspring) that either a male or a female would lose by providing care for the current brood. We

proceed as before, but note that our equality condition no longer holds: males and females do not have the same total number of broods. Instead, if males as a whole participate in X broods, females as a whole participate in only pX (this linkage between paternity and number of male matings was recognized by Werren *et al.* (1980), but they did not use it to link male versus female conditions). With each sex losing a fraction C of its future broods due to care of the current brood:

$$pb > \frac{pCX}{m} \quad (3)$$

$$b > \frac{CpX}{f} \quad (4)$$

Paternity now cancels out of the first (male) equation, but the equal reproduction constraint causes it to resurface in the second. This gives the identical result as inequalities (1) and (2): lower paternity means females are more easily selected to provide care than males.

The argument depends on males wasting some of their parental investment on non-relatives, incurring costs for no benefit. This assumes that males do not identify and exclusively aid their own true offspring in a brood, ignoring the others. Current evidence supports this assumption (Keller 1997).

3. SEXUAL SELECTION AND POTENTIAL REPRODUCTION

Another argument for why males provide less care is that they have greater potential reproduction, and hence more to lose if they concentrate on caring for a subset of their offspring (Clutton-Brock 1991). The model above appears to suggest that this argument is wrong, but in fact it is only incomplete, and the model shows what is necessary to complete it.

Again, it is necessary to distinguish the two kinds of arguments made. If we are simply asking whether a particular male should provide care to his current brood, then clearly his potential future reproduction should matter (Maynard Smith 1977). But if we are comparing the whole class of males with the whole class of females, the argument is more complicated. At first it appears to be wrong, because no matter how much greater the potential reproduction of males is, their average actual reproduction is constrained to be exactly the same as that of females, given an equal sex ratio. However, the argument can be made to work. We need to shift away from average males and females to the subsets of males and females who actually have a choice of providing care to their young. The subsets who have this choice are those who have mated and therefore have young available for care. The constraint remains the same; mated males reproduce the same total amount as mated females, so inequalities (1) and (2) still apply. But the calculations of the expected success of males and females (X/m , X/f) should exclude non-mating males and females, who are irrelevant to the particular question at hand. This is most easily accomplished by redefining m and f to be the numbers of males and females that mate (a more accurate model would also need to weight for frequency of

matings, but this is not required to establish the main point). The earlier conclusion that males will be less selected to provide care than females when $m < f$ now has an altered meaning; males are less selected to care if fewer of them mate than females.

This is a condition that will often apply as a consequence of the operation of sexual selection. As a rule, variance in male reproduction is higher than variance in female success (Bateman 1948). Sometimes this could be due to random factors only (Sutherland 1985) and when this is true, the argument that follows does not apply. But male variance may also be greater for biological reasons. Both female choice of males and male-male competition often involve social contests where a small edge over other males may translate into a large advantage. Male reproduction is closer to a winner-takes-all contest than is competition among females. Because of this, males may adopt risky strategies to try to become a top male, resulting in greater male mortality, so that $m < f$, and female care is favoured. But the mortality difference is not required; fewer males mating has the same effect. In such species, though average male and female reproduction remain equal, this is not true of the select subsets who mate, and only these individuals have the opportunity to be selected for parental care. The males involved in mating are a more select group, with higher expected reproductive success than the females involved in mating. If we use inequalities (1) and (2), but with m and f representing the numbers of males and females that mate, the higher male reproductive variance normally implies that $m < f$, and the inequalities therefore predict that males will tend to have greater costs of parental care, so parental care will evolve more readily in females.

To take a numerical example, suppose grouse leks consist of 20 males, and the top male obtains essentially all of the matings at that lek, which would amount to mating with 20 females if the sex ratio is at unity. Should males or females care for the young? The cost to an average male is irrelevant because average males do not mate and therefore have no real option of providing care. A top male, who does have the choice, should be much less willing than a female to part with a given fraction of his future success, because his expected success is 20 times greater than the female's.

This argument provides the desired link between the pre-mating and post-mating asymmetries in investment. If females invest more prior to mating, it sets up conditions conducive to sexual selection, both male competition and female choice (Bateman 1948; Trivers 1972). To the extent that sexual selection causes a greater variance in male success than female success, males will be less likely than females to provide more care after mating. The same positive feedback can work on post-mating care alone. As females provide more care, sexual selection on males intensifies (Clutton-Brock & Parker 1992), and this makes them even less likely to begin providing care. Conversely, if males begin to provide care for some reason, sexual selection on them will become less intense, and selection for them to engage in even more care may become easier.

It should be emphasized that these arguments are not meant to account for the entire distribution of parental care. Other factors that affect the costs and benefits have recently been reviewed (Westneat & Sherman 1993). To take an extreme example, in plants, the male is in no position to provide much in the way of parental benefits. Similarly, it has been argued that males of certain territorial fish can easily engage in parental care because they must stay on their territories to attract future mates, and defense of the young does not detract much from this goal (Williams 1975). These kinds of selective forces can still apply. The model presented here simply shows that there are two fairly general selective forces, stemming from probability of parentage and from sexual selection, that tend to promote female care and might therefore help explain its preponderance in nature.

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