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The battle of the sexes over the distribution of male surplus

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Abstract

Female primates carry and nurse the fetus, and thus have the first responsibility for rearing the offspring. Assuming males are at least equally adept at obtaining food, males might either share surplus food with females or consume the food themselves. The distribution of this surplus is the subject of a battle of the sexes. If females succeed in obtaining a large share of the surplus, then there is little size dimorphism between males and females; otherwise males might use the surplus themselves to become larger and stronger, and to engage in sexual competition with other males. Besides competing with males, females may compete with each other. Dependency may coincide with sexual competitiveness (sexiness). This paper introduces these ideas in a game theoretic setting and derives a simple bound, called the alpha male condition, on the male 'sexiness' required for a nonsupportive strategy to be worthwhile.

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1 Introduction

The position of women in technologically advanced societies generates numerous questions. Is there a 'glass ceiling'? Are women significantly disadvantaged because they have the babies and are likely to take a few weeks or a few years off from employment outside the home? Is there negative discrimination against women based solely on their gender and if so, why?

Or do females have opportunities for advancement that are unavailable to males? More generally, do females have a different set of strategies than males to employ in their interactions with other females and with males in the marketplace? Will women, because of their reputed special nurturing instincts, people-management skills and 'emotional intelligence' eventually dominate management of large organizations? These are questions that are subjects of intense emotional and academic debate, and they loom large in policy discussions. The questions seem to have no simple answers, in part because humans are highly intelligent and exquisitely subtle in their relationships with others.

In this paper, we try to step back from human nature and human problems and focus on evolution of primates in an attempt to begin to understand the differences between male and female competition and the strategies available to males and females. The analysis in this paper is intended to make some elementary but essential points from an evolutionary perspective. Our main thesis is that dependency may be an evolved strategy of females. Furthermore, sexual size dimorphism (the difference in size of males and females) may depend on whether females are successful at eliciting male parental support.

Let us begin by placing this thesis in the context of ideas from the literature on evolution. Evolution involves competition and a battle of the sexes. Physical and behavioural attributes that enhance reproductive prospects will spread by natural selection. But while sexual reproduction requires joint action, the characteristics most conducive to reproductive success for males and females are markedly distinct. If the female is able to care for the offspring herself, his reproductive success may be best served if she does so while he seeks out new opportunities to procreate. Her reproductive success may be best served if he devotes himself to providing support for her and her offspring while she takes advantage of passing opportunities to mate with other males, thereby increasing the genetic diversity of her offspring. Thus the reproductive success of the female and the male appear to be at odds: whereas that of the female requires the male to invest in parental care, the success of the male may require that he invest in the ability to attract many mates (which may involve the fighting off of other males). Hence, there is an evolutionary battle of the sexes. A key factor in this battle will be the female's ability to support herself and her young in the absence of male support.

Female primates carry the fetus, and nurse the infants. If females and males were equally efficient at gathering foods, then males may be able to produce a surplus of calories relative to females. There are apparently at least two ways in which such a surplus can be used. First, males can have larger body sizes and use the calories to maintain their own larger body sizes and to engage in male sexual competition for mates.[1] If males do not provide parental support, we hypothesize that the extra energy available to males is used up in male sexual competition.[2] It seems that typically, at least among primates, this sexual competition takes the form of increased size of males (see, for example, Mace 1992). Alternatively, males can share food with females, in which case we can expect less sexual size dimorphism – smaller differences in the sizes of females and males.[3] This reasoning is borne out by observed sexual size dimorphism among primates – in general, the more females provide for their own offspring, the greater the size difference between females and males.[4] The evolutionary battle of the sexes is reflected in a battle over the division of the surplus generated by males.

What strategies females may have evolved to capture the surplus generated by males appears to have been little investigated in the literature. In this paper, we examine one possibility; females, by being slightly less able to raise their offspring themselves, may put males in the position where the most successful genes are

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[1] A numeraire is required to compare the production of males and females; following other literature we use calories as the unit of comparison. Kaplan and Robson (1999) provides an interesting study of the production of Ache males and females, compared with their consumption of food, measured in calories. The Ache are an indigenous population of Paraguay.

[2] It may be that the larger size of the male also makes him better adapted to some other tasks than the female, for example, territorial defense, so he may expend more energy than the female on such tasks.

[3] The absence of size dimorphism appears typical of monogamous primates. See, for example, Mace (1992) for a comparison between the extent of size dimorphism in various primates, humans included. The fact that there is some dimorphism seems to convince some anthropologists that humans are basically polygynous (cf. Fleagle 1999). The fact that the extent of human sexual size dimorphism is relatively small convinces others that man is near-monogamous. While great diversity in human behaviour has been observed, perhaps most economically successful societies are near-monogamous. In a widely reported study, Dr. Charles Nunn and his collaborators (Nunn, Gittleman and Antonovics 2000) document a positive relationship between promiscuity and normal high white blood cell counts of primates and observe that humans have white blood cell counts that are consistent with near-monogamy.

By ‘monogamy’ we typically mean that males and females are, on the whole, ‘faithful to the nest’. Each contributes care to one particular family unit but each may take advantage of passing opportunities to have more genetically varied offspring and, for the male, to have some offspring ‘on the side’ to which he provides little parental support.

[4] Note that this is similar but has quite a different flavor than the frequent observation that the more polygynous a species, the greater the sexual size dimorphism (cf., Gould and Gould 1997). The outcomes are the same but the root causes differ. Here, we begin with the observation that females may benefit from male parental support. To the extent that males are using their time and energy to provide this support, they do not have time and energy to engage in conflict with other males. Thus, the benefits of large size, relative to other males, to enable a male to win battles with other males are less important to evolutionary selection.

those that favor male parental support.[5]

The idea that females have evolved to be dependent in certain ways may explain the fact that human females typically have less upper body strength than males and, because of this, are typically unable to defend themselves against attack by males. We hasten to note that none of this suggests that females are less able to function in the modern world of high tech and large social and economic organizations. In fact, the opposite may well be true; insofar as females may have had to evolve strategies to elicit male support and resolve conflicts with males in a nonviolent manner (in view of the male's greater physical strength), females may in fact be superior at various skills that are highly valued in modern societies.[6]

If females are dependent on male support to raise their offspring, then the quality and quantity of that support is important. It is not clear that the support of one male is particularly important. But since males have limited resources it would seem natural that females compete with each other for mates who will be faithful to the nest.[7] Dependency may also be important for this female-female competition. If a male sires offspring with two females, one who needs his support and another who does not, then all else being equal, he will maximize his fitness by providing support to the dependent female. If a female can slightly decrease her own ability to raise her offspring by herself and, by so doing, convince her partner that his offspring need his support, then this may be a winning strategy – by a small decrease in her own capability she gains the support of another person.

This paper, the first in a planned series investigating the evolutionary foundations of female competition, introduces the idea that human evolution may have involved dependency of females and co-evolution of responsiveness of males to this dependency. In the context of a simple model we establish a relationship between the 'sexiness' required by a male to benefit from playing the nonsupportive strategy of pursuing multiple mates and a ratio measuring the importance of male parental support.

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[5] A female's dependency does not imply helplessness per se; indeed it may largely arise through the dependency of the offspring she has in tow.

[6] In fact, many evolutionary theorists and biologists take the view that human intelligence was an evolved outcome resulting from the demands of hunting. Hrdy describes this view as follows: "Success depended on special male skills: visual-spatial capacities, stamina, stalking abilities and especially cooperation" (Hrdy 1989, p.5). In contrast, Hrdy's own research, and other recent research (cf., Dunbar 1996), accords a larger role in the development of intelligence to socializing behaviours.

[7] Since the time (and, in modern societies, the money) of each male is limited, there is an opportunity cost to a female in choosing any particular male and this opportunity cost is higher, other things equal, the more dispersed his parental support. Contrast this with situations where male parental support is irrelevant. In this case, each female can do no better than mate with the sexiest male – the one who is likely to sire sexy offspring.

2 A simple evolutionary battle of the sexes

We suppose that females have two possible strategies, 'dependent', D; or 'independent', $\overline{D}$. If a female chooses D she is less able to raise her offspring by herself than she is if she chooses $\overline{D}$. A male also has two choices, whether to be supportive, S, or nonsupportive, $\overline{S}$. Playing $\overline{S}$ is to be interpreted as the strategy of constantly seeking new opportunities to reproduce and investing in the pursuit of females rather than in the care of existing offspring and current mates. We can interpret the strategy $\overline{S}$ as either nonsupportive or roam while the strategy S can be interpreted as supportive and 'faithful to the nest'. If the male chooses S he can perhaps gather food for the female and her offspring and protect her and her offspring against other males and predators. Our analysis treats the problem of local equilibrium on the game as played between a given heterosexual pair, not with equilibrium outcomes at the population level.[8]

A female who plays the dependent (D)-strategy against a male playing the supportive (S) strategy has fecundity (fitness) $\tilde{A}_F(D;S)$. The fecundity of such a female will be (marginally) higher than $\tilde{A}_F(\overline{D};S)$, the fecundity of an independent ($\overline{D}$) female playing against a supportive male, because of the investment made by the latter female to be capable of independence. Interpreting this in a modern setting, one might imagine the female playing $\overline{D}$ as a woman who chooses to delay childbirth while she finished her studies and who chooses to learn algebra as a teenager rather than babysitting to earn more money for clothes.[9] In evolutionary terms, genes that led females to develop more muscle mass rather than wide hips, great for childrearing but less advantageous for running, would constitute an example of the evolution of independent females. Of course, an independent female's fecundity will still benefit from male support, and therefore $\tilde{A}_F(\overline{D};S)$ will be larger than $\tilde{A}_F(\overline{D};\overline{S})$, the fecundity of an independent female playing against a non-supportive ($\overline{S}$) male. Finally, independence allows a female to do better than dependency when playing against a non-supportive male, and therefore $\tilde{A}_F(\overline{D};\overline{S})$ will be larger than $\tilde{A}_F(D;\overline{S})$, the fecundity of a dependent female playing against a non-supportive ($\overline{S}$) male. We thus have the following chain of inequalities:

$$\tilde{A}_F(D;\overline{S}) < \tilde{A}_F(\overline{D};\overline{S}) < \tilde{A}_F(\overline{D};S) < \tilde{A}_F(D;S) : \qquad (1)$$

Next we consider male fitness $\tilde{A}_M(¢;¢)$. In our expressions for male fitness, we assume that an individual is playing against only one other individual at a time.

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[8] Mating assortment induces closure at the level of the population, where ESS equilibria can be studied; we take up this analysis elsewhere.

[9] Of course, an individual female is not always in control of the choice between dependence and independence. For instance, socioeconomic conditions might prevent her from developing the skills required for independence. However, we are concerned here with the reproductive success associated with the respective strategies, in order to analyse which combinations will be most likely to spread on average. We thus tacitly assume that socioeconomic conditions exert no significant bias. In this context, a player's choice should be viewed as a convenient fiction, which is standard in game theory.

The fecundity of a male who is supportive and faithful to the nest equals that of the female he is playing against. Thus

$$\begin{cases} \psi_M(D,S) = \psi_F(D,S) \\ \psi_M(\overline{D},S) = \psi_F(D,S) \end{cases} . \tag{2}$$

The non-supportive male, on the other hand, has a fecundity which depends on x, his ability to attract mates, and the strategies played by these mates:

$$\psi_M(\gamma,\overline{S}) = x\left(\gamma\psi_F(D,\overline{S}) + (1-\gamma)\psi_F(D,\overline{S})\right) \tag{3}$$

where $\gamma \in [0,1]$ is the proportion of dependent mates. This parameter depends not only on the composition of the female population in terms of strategies played, but also on the outcome of various competitions among males for access to females, among females for access to males, and among females and males. For the local equilibrium results of this paper, we refrain from modelling the balance of power involved in all these conflicts, and leave γ as an unknown 'lumped' parameter.

The battle of the sexes game can now be analysed by considering in turn the three situations in which a male may find himself. First, the male's 'sexiness' x may be sufficiently large to fulfil the condition $\psi_M(\gamma,\overline{S}) > \psi_F(D,S)$. Such a male will have a greater fecundity playing $\overline{S}$ than S, from (2). Against such a male the female maximizes her fecundity by playing $\overline{D}$, from (1), and the outcome is $\{\overline{D},\overline{S}\}$.

We next turn to the case where $\psi_F(\overline{D},S) < \psi_M(\gamma,\overline{S}) < \psi_F(D,S)$. The optimal male choice is now dependent on the strategy played by the female. If the male plays S, the best reply of the female is to play D, dependent, while if the female plays D, the best response of the male is S, which means that $\{D,S\}$ is a strict Nash equilibrium.[10] The outcome $\{\overline{D},\overline{S}\}$ is also a Nash equilibrium (with the $\overline{D}$ referring to the roaming male's 'nominal' mate). This outcome, however, is far less advantageous to the female. If the proportion of females opting for dependency is large, γ is likely to be close to unity, which induces the situation where $\psi_M(\gamma,\overline{S}) < \psi_M(\overline{D},S)$. In this case, supportive males do better than non-supportive ones, by (1) and (2). Given that the male plays S, the female does best by playing D, and the outcome is again the strict Nash equilibrium $\{D,S\}$.

Special difficulties arise in the case of equalities. When $\psi_M(\gamma,\overline{S}) = \psi_F(D,S)$, the male's choice between S and $\overline{S}$ is indifferent if the female plays D. By (1), the female's fitness when playing D could be either larger or smaller than when playing $\overline{D}$, depending on the male's choice. If the male chooses S, the female does best by choosing D. If the male chooses $\overline{S}$, the female should play $\overline{D}$, to

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[10] That is, if the female chooses D and the male chooses S, then any change of strategy of either player will make that player strictly worse off.

which $\bar{S}$ is the best male reply. Thus both the outcomes $\{D; S\}$ and $\{\bar{D}; \bar{S}\}$ are Nash equilibria. If we knew the statistics of the male's choice when the female plays D, together with the differences between various female fecundities, we could calculate the female strategy with the highest expected fecundity.

Similarly, when $\psi_M(\gamma; \bar{S}) = \psi_F(\bar{D}; S)$, the male's choice is indifferent if the female plays $\bar{D}$. Again, playing $\bar{D}$, the female might do either better or worse than when playing D, depending on the strategy played by the male. If the male elects to play S, the best reply is D, to which S is the best male reply. Thus, again the outcomes $\{D; S\}$ and $\{\bar{D}; \bar{S}\}$ are both Nash equilibria.

From this game-theoretic analysis we conclude that the male should generically play $\bar{S}$ only when his sexiness is sufficiently high, that is, such that $\psi_M(\gamma; \bar{S}) > \psi_F(D; S)$ holds true. We call this the α-male condition; it specifies how large a male's sexiness x – his ability to attract 'opportunity mates' in addition to a nominal mate – must be so as to render the non-supportive strategy worthwhile. When $\gamma = 1$, this condition is equivalent by equation (3) to

$$x > \frac{\psi_F(D; S)}{\psi_F(D; \bar{S})} \tag{4}$$

(when $\gamma < 1$, this condition is sufficient but not necessary for α-maleness).[11] Since $\psi_F(D; S)$ is the largest female fecundity value, α-males must have $x > 1$ regardless of γ. When the sex ratio in the population is 1:1, the prerequisite $x > 1$ implies that α-males must have an increased sexual competetiveness. The ratio $\psi_F(D; S)/\psi_F(D; \bar{S})$ expresses how much male support matters for a female. This ratio will be large when offspring require constant care over a prolonged period. We have argued that this is the case for humans, which would imply that α-males in humans would have to be very sexy indeed. This may explain the relative paucity of polygynous human societies as well as the absence of pronounced sexual dimorphism in our species.

3 Conclusions

The following considerations suggest that male support is important in humans. The unique intelligence which characterizes our species appears to require that human infants have large heads, so large, in fact, that the human newborn, unlike other newborn primates, is unable to support the weight of his head. Thus, unlike other primates, since it cannot simply cling to its mother as she goes about 'earning her living', a human baby needs to be cradled. The large size of the cranium also means that, to allow passage through the birth canal, human infants are born 'early' relative to other primates. Consequently, human

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[11] Of course at the population level, with an equal sex ratio on average males and females will have the same fitness. The bound on x above applies to any particular male in a population.

babies need constant care, and it is several years after birth before a human child can make his own way in the world. It is clear that the mother can benefit greatly from help in raising her offspring; in fact, male parental support may be crucial. In evolutionary time, those females whose genes better facilitate the elicitation of male parental support can have more surviving offspring; such genes may spread more quickly than genes that enable females to be more able to raise their offspring alone. Thus, when male parental care is important, evolution may favour females who are able to attract males who are faithful to the nest – that is, although perhaps taking advantage of passing opportunities to mate, without commitment, with other females, males who provide support and care for the female and her offspring.

The simple model of a normal form game presented in this paper can be interpreted as illustrating a battle of the sexes fought over the surplus generated by males, a surplus which arises naturally from the fact that many of the burdens of raising offspring tend to fall on the female. It is reasonable to assume that female fitness would be enhanced from expenditure of this surplus on parental investment, while male fitness may benefit from expenditure on body growth (that is, on sexual competitiveness), insofar as females are able at all to raise offspring without support. If females control male access to procreation, and are able to exact some sort of guarantee before allowing the male access, nonsupportive males will have no fitness whatsoever. On the other hand, if males are able to enforce sexual contact, investment in bodily strength confers fitness (both in combating male rivals and perhaps in ensuring female cooperation). In between these extremes, if males who are 'sexy' are likely to have sexy offspring and if male parental support is not absolutely essential, the reproductive patterns of humans may be an expected consequence. When the state provides more support for females who are unable to support themselves and their offspring, then it seems that more males are likely to play nonsupportive, $\overline{S}$.

A number of researchers in biology have discussed the importance of female strategies and male parental support among primates, cf., Dunbar (1992,1995), Hrdy (1989) and references therein. Clutton-Brock (1991) studies the evolution of parental care. More recently, modern treatments have taken into account evolutionary battles of the sexes; see, for example, Mylius (1999). Our treatment suggests that dependency may be an evolved female strategy and male supportiveness may have co-evolved. It also suggests that the importance of male parental support is a root determinant of whether there is sexual size dimorphism. It is of course dangerous to strictly apply evolutionary reasoning to human behaviour, which is very complex and also very adaptable. Indeed, among humans (and certain primates) many sorts of marital patterns have been observed. We speculate that economic conditions are crucial, in particular, whether the society and economic conditions can support the offspring if nearly all males and females are monogamous.[12]

Our model only considers the local outcomes of the game of dependency and support played between males and females. Of course, the incentives at the local level imply a direction of change at the global level. We will analyze this further in a forthcoming paper.

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[12] Siow (1998) considers related issues from a theoretical perspective.

References

[1] Clutton-Brock, T. H. The evolution of parental care with original drawings by Princeton, NJ.; Oxford : Princeton University Press, 1991.

[2] Dunbar, R. (1996) Gossip, Grooming and the Evolution of Language, Faber and Faber Ltd. London.

[3] Dunbar, R. (1992) "Mating and parental care," in The Cambridge Encyclopedia of Human Evolution, eds. S. Jones. R. Martin and D. Pilbean, Cambridge University Press, Cambridge, UK., 150-152.

[4] Fleagle, J.G. (1999) Primate Adaptaion and Evolution, Second Edition, Academic Press, San Diego/London/Boston/New York/Sydney/Tokyo/Toronto.

[5] Gould, J.L. and C.G. Gould (1997) Sexual Selection; Mate Choice and Courtship in Nature, Scientific American Library, New York.

[6] Hrdy, S.B. (1989) The Woman that Never Evolved, Harvard University Press, Cambridge, Massachusets and London, England.

[7] Kaplan, H. and A.J. Robson (1999) "The co-evolution of human longevity and intelligence in hunter-gatherer economies," typescript.

[8] Landers, J. (1992) "Reconstructing ancient populations," in The Cambridge Encyclopedia of Human Evolution, eds. S. Jones. R. Martin and D. Pilbean, Cambridge University Press, Cambridge, UK., 402-405.

[9] Mace, G. (1992) "Differences between the sexes," in The Cambridge Encyclopedia of Human Evolution, eds. S. Jones. R. Martin and D. Pilbean, Cambridge University Press, Cambridge, UK. p. 52-55/

[10] Nunn, C.L., J. L. Gittleman and J. Antonovics (2000) "Promiscuity and the primate immune system," Science November 10; 290: 1168-1170.

[11] Siow, A. (1998) "Differential fecundity, markets and gender roles," Journal of Political Economy, 106 (2), April 1998, 334-354.