

**FEMALE COMPETITION, EVOLUTION
AND THE BATTLE OF THE SEXES**

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Female competition, evolution, and the battle of the sexes^a

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Abstract

As female primates carry and nurse the fetus, it naturally falls on them to rear the offspring. On the assumption that males are at least equally adept at obtaining food, it follows that they generate a surplus which they might either share with females or consume themselves. This choice lies at the heart of an evolutionary battle of the sexes. If females succeed in obtaining a large share of the surplus, there is little scope for size dimorphism between males and females; otherwise males can use the surplus to sustain larger and stronger bodies, which are advantageous in sexual competition with other males. Besides competing with males, females may compete with each other. Moreover, dependency may coincide with sexiness and such dependency can persist. This paper examines these ideas in a game-theoretic setting.

1 The female in evolutionary theory

The position of women in technologically advanced societies generates numerous questions. Is there a 'glass ceiling'? Are women significantly disad-

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vantaged 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 gender or do women simply have different preferences, abilities and opportunities?

Or does modern society provide females with 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, even 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 questions are subjects of intense emotional and academic debate and they loom large in policy discussions. But there seems to be no simple answers, in part because humans are highly intelligent and exquisitely subtle in their relationships with others and in part because of the different roles of males and females in child rearing. Here we take up a more straightforward question that does seem to be crucial to the foregoing questions: How should a female divide her resources between generating economic power and mothering, while relying on male parental support?

To address these questions, we assume that a female faces a trade off between (i) using her own resources to generate economic power for the support of herself and her offspring and (ii) using those resources more intensively for mothering and relying more heavily on male parental support. A male faces a trade off between (i) investing his resources in his attractiveness to females (that is, engaging in male sexual competition) and thus increasing the number of females with whom he mates and (ii) investing in the care of his own offspring, so that he can have more offspring with one mate. We analyze these trade offs using two different models. Our first model indicates that the extent to which males invest in sexual competitiveness (size, for example) is inversely correlated with female dependence. An exception is when the rearing of offspring is not cost-intensive, in which case females will always be fully dependent. When offspring are expensive, as they are likely to be with humans, female independence correlates directly with female ability to generate income.

We next analyze a severe model where the trade off for females is either to be dependent, and unable to raise offspring themselves, or to be independent and capable of raising offspring themselves. The results suggest that full female dependence on male support will persist in those settings where females are less well suited to food gathering (or income acquiring) than males.

Before proceeding to the analysis, let us put these trade offs in a more

general context. Evolution involves competition and a battle of the sexes. On the basis of natural selection we expect that those male and female characteristics that contribute to the ability to attract mates (sexiness) and promote reproductive output will spread through the population. An essential asymmetry arises between males and females, however, because the female is more closely associated with offspring during an extended period of time. During this time she makes a sizeable investment of resources in the offspring. Thus, a female cannot abandon her offspring without seriously reducing her fitness; in economic terms, the opportunity cost to the female of nonsurvival of any one of her offspring is high. In contrast, the opportunity cost to a male of abandoning one or more of his offspring may be quite low and especially so if females are independent.¹ Thus, while sexual reproduction requires joint action, the characteristics that tend to promote reproductive success for males and females are distinct.

If the female is able to care for the offspring herself, the fitness of her mate is enhanced if she does so while he seeks out new opportunities to procreate. In contrast, her fitness is enhanced if her mate devotes himself to providing support for herself and her offspring while she takes advantage of passing opportunities to mate with other males, thereby increasing the genetic diversity and quality of her offspring. Thus, the fitness of the female may increase with her ability to garner male support, whereas the fitness of the male may be greater when he maximizes the number of females he impregnates. The two are at odds: whereas the former requires the male to invest in parental care, the latter may require the male to 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 make large investments in their offspring. They produce the eggs, carry the fetus, and nurse the infants; these are all investments that the male need not make. If females and males were equally efficient at procuring foods through hunting and gathering, it follows that males must be able to produce a surplus relative to females. Following other literature, let us take calories as a numeraire to measure the production of females and

¹In some species, desertion of offspring by the female appears to be an important strategy. McNamara et al. (2000) consider species that have one or more broods each year during a breeding season of finite length. In their analysis, the female chooses between caring for or abandoning each brood after the male has chosen between support or non-support, with his best choice dependent on the expected number of matings in the remainder of the breeding season.

males.² There are at least two ways in which the surplus calories of males can be used. Males can use surplus calories to maintain their own larger body sizes and to engage in male sexual competition for mates. Alternatively, males can share food with females, in which case we can expect less sexual size dimorphism – less difference in the sizes of females and males. The absence of size dimorphism appears typical of monogamous primates.³ The evolutionary battle of the sexes is reflected in a battle over the division of the surplus generated by males.

Thus, suppose that our early female ancestors had not succeeded in persuading males to share food and provide male parental support and that males were at least as efficient at procuring food as females. If males had no additional energy requirements we would have a contradiction: males would have more energy available to them but fewer uses for that energy than females. In particular, if males do not provide parental support, we hypothesize that the extra energy available to males is used up in male sexual competition.⁴ It seems that, at least among primates, this sexual competition typically takes the form of increased size of males.⁵ 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 difference in size between the females and the larger males.⁶

²The use of calories as a numeraire to measure output of gathering and hunting activities also appears in Kaplan and Robson (1999), for example. We discuss their research and its implications for ours in a concluding section.

³The absence of large 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. 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 behavior 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 near-monogamy and even by ‘monogamy’ we 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 whom he provides little parental support.

⁴It may be that the larger size of males leads to further specialization of males and females. Males may take leading roles in defence against territorial predators from other species, for example. We do not examine this question.

⁵See Fleagle (1999), p. 307 or Mace (1992), p. 54,

⁶Note that this is quite distinct from the frequent observation that the more polygynous

What strategies females may have evolved to capture the surplus generated by males has been little investigated in the literature. In this paper we propose that one possibility is that females, by being slightly less able to raise their offspring themselves, may put males in the position where they evolve to provide male parental support.⁷ (In the following, this is apparent in equation (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.⁸ Dependency may also be important for this female-female competition. If a male sires offspring with more than one female and one needs his support while the other does not, 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 he will maximize his fitness by being faithful to her nest, then this may be a winning strategy – by a small decrease in her own capability she gains the support of another person.

This paper, one in a planned series investigating the evolutionary foundations of female competition, continues the idea introduced in Wooders and van den Berg (2001) in a local equilibrium setting, that dependency of females and co-evolution of responsiveness of males to this dependency may be a feature of the evolution of humans. It also relates sexual size dimorphism to female dependency, which itself is connected to the needs of offspring. We note that a number of researchers in biology have discussed the importance

a species, the greater the sexual size dimorphism (cf. Gould and Gould 1997). While the outcomes are the same, the root causes differ. Here, our starting point is the observation that females and their offspring may benefit from male parental support. To the extent that males devote resources to provide this support, they do not have these resources available to engage in conflict with other males. The benefits to males of large size, relative to other males are less important to evolutionary selection when more of the resources available to males are required for parental support. If, for example, the support of two parents is essential for the survival of offspring, then males cannot benefit from competition with other males for multiple mates.

⁷Of course females may become more dependent when their offspring are more dependent.

⁸Since the time (and, in modern societies, the money) of each male is limited, there is an opportunity cost of 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 have sexy offspring.

of female strategies and male parental support among primates, cf. Dunbar (1992,1995), Hrdy (1989), McNamara et al (2000) and references therein. Our research differs significantly in that our focus is on the trade offs between sexiness and parental support, and the strategies females may use to elicit male support.

2 The trade off between male sexual competitiveness and male parental support

Let us assume that females are able to set their allocation of time between gathering of calories and carrying/nurturing offspring. Let $y \in [0; 1]$ denote the fraction of time females spend on the gathering of calories. The remainder $1 - y$ of their time is spent on raising offspring. We assume that each offspring requires a time period T_0 during which the female is unable to gather calories; this period T_0 corresponds to the last phases of pregnancy plus the initial period of childcare. The rate at which females produce offspring is $(1 - y)/T_0$. Since T_0 is a constant we can represent the female's fitness by $(1 - y)$.

Let $x \in [0; 1]$ denote the fraction of the calories generated by a male that he invests in acquiring sexual competitiveness; the remainder $(1 - x)$ is spent on his offspring. We assume that males compete for access to females. A male's fitness is the product of the fitness of his mate(s) times the number of his mates. To find this number, let $K(x)$ denote the sexual competitiveness of a male who spends a fraction x on the development of such competitiveness; and let \bar{K} denote the average competitiveness of the males. Then the expected number of mates is

$$\frac{K(x)}{\bar{K} N_M} N_F$$

where N_M is the number of males in the population and N_F is the number of females. The flux of energy per time (power) $P_S(x)$ received by each of the male's mates is

$$P_S(x) = (1 - x) \frac{\bar{K} N_M}{K(x) N_F} P_M$$

where $P_M > 0$ is the power generated by a male which he distributes between competitiveness and parental support. We assume P_M to be equal for all the males in the population.

A female's choice of time allocation y is constrained by the support she receives from her mate, characterized by x :

$$(1 - y) \frac{U_0}{T_0} \leq y P_F + P_S(x) \quad (1)$$

where $P_F > 0$ is the power (calories per time) generated by the female when she is foraging, and where U_0 is taken to be the minimal amount of energy required by each offspring. If the male supplies (more than) sufficient support, that is, if

$$P_S(x) \geq \frac{U_0}{T_0};$$

the female is able to set $y = 0$, which gives her the maximal fitness 1, and the male a fitness $(K(x)N_F) = (KN_M)$. Otherwise, she has to spend at least a fraction

$$y(x) = \frac{U_0 - T_0 - P_S(x)}{U_0 - T_0 + P_F} \quad (2)$$

of her time on foraging. To maximize her fitness $(1 - y)$, she should spend no more than this fraction of time on foraging; we will assume that all females behave in this manner.⁹ The male's fitness in this case is $(1 - y(x))(K(x)N_F) = (KN_M)$.

It is convenient to use P_M as a unit of power. Thus we define dimensionless parameters

$$\hat{\gamma} = \frac{P_F}{P_M} \quad \text{and} \quad \frac{1}{2} = \frac{U_0 - T_0}{P_M}; \quad (3)$$

The parameter $\hat{\gamma}$ expresses how well females are suited to foraging compared to males. The parameter $\frac{1}{2}$ expresses the cost-intensiveness of offspring. If $\frac{1}{2} > 1$, a male devoting all his power to a single female who does no foraging herself is unable to supply her with the energy she needs. We now analyze the ES (evolutionarily stable) values of x , under two further assumptions: (i) equal sex ratio, $N_F = N_M$; and (ii) sexual competitiveness is directly proportional to investment $K(x) \propto x$.

Consider the fitness of a male who invests a fraction x of the energy he generates in sexual competitiveness, in a population in which the average

⁹Thus we assume that females adopt in life history time to whatever their needs dictate; in evolutionary time this adaptation is instantaneous. Hence females can be described by equation (2).

such investment by a male is \bar{x} . We denote this fitness $f(x; \bar{x})$. On the above assumptions and scaling, we obtain:

$$f(x; \bar{x}) = \begin{cases} \frac{x}{\bar{x}} & x \leq \frac{\bar{x}}{\frac{1}{2} + \bar{c}} \\ \frac{1}{\frac{1}{2} + \bar{c}} + \frac{x}{\bar{x}} \left(\frac{\bar{c}}{\frac{1}{2} + \bar{c}} \right) & x > \frac{\bar{x}}{\frac{1}{2} + \bar{c}} \end{cases} \quad (4)$$

where $x = \frac{\bar{x}}{\frac{1}{2} + \bar{c}}$ corresponds to support which is (more than) sufficient to support a female at $y = 0$. We show in Appendix A that the ES values of x are as follows:

$$\hat{x} = \begin{cases} \frac{1}{2} & 0 < \frac{1}{2} \cdot \frac{1}{1 + \bar{c}} \\ \min\left\{1, \frac{1}{1 + \bar{c}}\right\} & \frac{1}{2} > \frac{1}{1 + \bar{c}} \end{cases} \quad (5)$$

with corresponding values for the female's foraging fraction:

$$y(\hat{x}) = \frac{\frac{1}{2} + \hat{x} \cdot \frac{1}{1 + \bar{c}}}{\frac{1}{2} + \bar{c}} \quad (6)$$

The dependence of \hat{x} and $y(\hat{x})$ on the parameters $\frac{1}{2}$ and \bar{c} is shown in Figure 1. Male support is only provided when $\bar{c} < 1$. Male support is represented as a darker tone (black: $x = 0$; white: $x = 1$): Males need to provide more support as females have lower food-gathering ability (low \bar{c}) and as offspring require a higher investment of power (high $\frac{1}{2}$). Females have to rely entirely on their own food gathering ability when they are more adept at gathering food than males ($\bar{c} > 1$). Female dependence is represented as a darker tone (white: $y(\hat{x}) = 1$; black: $y(\hat{x}) = 0$.) Females can only rely completely on male support if $\frac{1}{2} + \bar{c} < 1$; otherwise they need to spend some portion of their time on foraging. This analysis suggests that male parental support may be enforced by the female's relative lack of food gathering capacity, while some degree of independence is imposed on the females when offspring are energy-intensive ($\frac{1}{2} > 1$), regardless of the female's relative food gathering capacity \bar{c} .

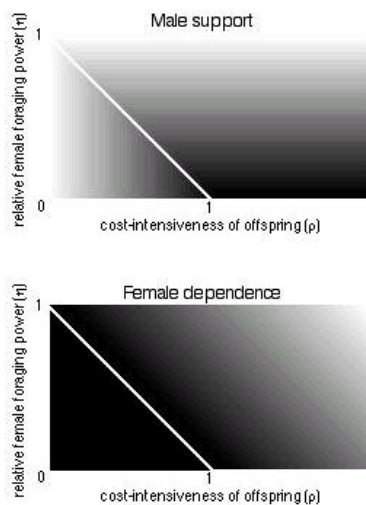


Figure 1:

Male support and female dependence.

Of course on the slower evolutionary time scale, the parameters $\frac{1}{2}$ and $\hat{\rho}$ might change. Changes in $\hat{\rho}$ on this time scale reflect alterations in anatomy or physiology or the environmental considerations, such as the characteristics of the workplace, which affect $\hat{\rho}$, the relative food gathering ability of females.

3 A severe model with female dependence

In the previous section we assumed that mating assortment was governed by male sexual competition for access to the females. Here we examine the opposite assumption that females control mating and assortment and that the flows of energy devoted to offspring are governed by female sexual competition for male parental support. For the sake of simplicity, we assume that a female makes a lifetime commitment to one of the following strategies: either she forgoes the development of food gathering (more generally, income earning) ability in exchange for an increased ability to garner male support or she develops food gathering capabilities and gives up a competitive edge in female sexual competition.¹⁰ Can dependent females trade off the ability

¹⁰We need not assume that the strategies are genetically hard-wired; for the purposes of our analysis it is immaterial whether a parent imbues a child with their strategy choice

to attract male support –sexiness – against the ability to single-handedly support their own offspring? In the following, we show that for a very severe model, where dependent (but sexy) females cannot raise any offspring at all without male support, there are population equilibria with positive proportions of dependent females.

There are two male strategies: supporter (S) and non-supporter (\bar{S}). S-males invest power in the propagation of the S-strategy, whereas \bar{S} -males do not, and rely on the power contributed by their female partners. There are two female strategies: dependent (D) and independent (\bar{D}). D-females have no earning power, and rely on male partners for support in propagating their strategy by raising offspring. \bar{D} -females have earning power, but trade this off against a lowered ability to attract S-male partners.

A traditional view in human societies has been that males should be S, and females should be D. The first question we ask is whether (all S, all D) is the single, stable equilibrium of the evolutionary dynamics that act on the four strategies. More specifically, we would like to characterize the socio-economic conditions under which this state of affairs holds true. This consideration naturally leads to further questions: in which societies is \bar{D} the dominant strategy for females? Under what conditions can we expect \bar{S} to be a dominant strategy?

3.1 Pay-offs to the four strategies

Let $f_S \in [0; 1]$ be the fraction of supportive males and let $f_D \in [0; 1]$ be the fraction of dependent females. We assume that D-females attract a fraction

$$\frac{\frac{3}{4}f_D}{1 + (\frac{3}{4} - 1)f_D}$$

of the S-male power input toward propagation. This formula is derived as follows. Let \hat{A}_D be the rate at which D-females emit sexual signals to S-males, and let $\hat{A}_{\bar{D}}$ be the rate at which \bar{D} -females emit such signals (where we assume all signals to be of equal strength, which is not a real restriction). Suppose that there are N_F females. Consider an S-male who chooses a partner upon receiving of a sexual signal. The probability that the female in question is D is found by dividing the rate at which the male receives signals from D-females, $\hat{A}_D f_D N_F$, by the rate at which he receives signals from all females, $\hat{A}_D f_D N_F + \hat{A}_{\bar{D}}(1 - f_D)N_F$. The result is the above formula, with $\frac{3}{4} = \hat{A}_D = \hat{A}_{\bar{D}}$. We call $\frac{3}{4}$ the ‘sexiness ratio’. We assume $\frac{3}{4} \geq 1$, with equality

by endowing them with a particular gene, or by impressing certain morals on them. In this sense, we are actually concerned with the adaptive dynamics of ‘memes’.

occurring only if \bar{D} -females have no earning power. The condition $\frac{3}{4} > 1$ when \bar{D} -females do have some earning power reflects our basic assumption that sexual attractiveness is trade off against earning power.¹¹

We assume that the number of males N_M is equal to the number of females N_F , and that the following number of S-males mate for life with \bar{D} females:

$$f_S N_M \frac{1 - f_D}{1 + (\frac{3}{4} - 1)f_D} :$$

This leaves the following number of \bar{D} -females unmatched to S-males

$$(1 - f_D)N_F - \frac{f_S}{1 + (\frac{3}{4} - 1)f_D} N_M :$$

We assume that these females mate with \bar{S} -males, not necessarily for life. The remainder of the S-males mates with D-females, though not necessarily for life, since the D-females may be 'overmatched' (as $\frac{3}{4} > 1$). \bar{S} -males and D-females cannot mate successfully, as neither contributes power to parental support.

Each S-male contributes an amount P_M of power toward propagation, and each \bar{D} -female contributes an amount $P_F = \lambda P_M$ of power. Here $0 < \lambda < 1$, which is now taken to reflect the trade off between attractiveness and earning power. The condition $\lambda < 1$ does not express female inferiority, but rather that females have to forgo some productive power in order to gain increased sexual attractiveness. \bar{S} -males and D-females do not contribute to earning power. The equal sex ratio ($N_F = N_M$) implies that the reproductive pay-off is equally shared out between the two strategies.

The offspring of S-males receive the following investment of power:

$$f_S N_M P_M + f_S N_M \frac{1 - f_D}{1 + (\frac{3}{4} - 1)f_D} \lambda P_M$$

¹¹Our assumed correlation between independence and sexual attractiveness should not be taken to imply that we assume that independent, career-making women are inherently less attractive, either because men consider professional competence unfeminine, or, worse, because unattractive women are compelled to seek an independent existence. What we mean rather is that an investment of time and effort in generating the potential to earn is at the expense of the generation of sexual signals, particularly during an early phase in life when relationships are built. We view the trade off as having a basic mechanistic, rather than a normative, basis. We certainly do not intend to say that the earning power of a female is sexually unattractive in and of itself.

where the first term is due to the S-males themselves, and the second to their \bar{D} partners. Half of this goes toward the S-strategy; and therefore the following equation obtains for Z_S , the per capita pay-off for the S strategy:

$$Z_S = \frac{\mu}{1 + \frac{(\frac{3}{4}i - 1)f_D + 1 - f_S}{1 + (\frac{3}{4}i - 1)f_D}} + \frac{\eta}{2} P_M : \quad (7)$$

The \bar{S} -strategy feeds entirely of the earning power of \bar{D} -females unmatched to S-males; their per capita pay-off is thus given by:

$$Z_{\bar{S}} = \frac{1 - f_D}{1 - f_S} \left(\frac{(\frac{3}{4}i - 1)f_D + 1 - f_S}{1 + (\frac{3}{4}i - 1)f_D} \right) + \frac{P_M}{2} : \quad (8)$$

The investment of power in offspring of D-females is due to S-males exclusively. The per capita pay-off works out as follows:

$$Z_D = \frac{\frac{3}{4}f_S P_M = 2}{1 + (\frac{3}{4}i - 1)f_D} : \quad (9)$$

\bar{D} -females, naturally, have their own contribution as well as some of the S-male support:

$$Z_D = \frac{\mu}{1 + (\frac{3}{4}i - 1)f_D} + \frac{\eta}{2} P_M : \quad (10)$$

3.2 Nullclines and equilibria

Making minimal and natural assumptions on evolutionary dynamics based on the pay-offs, we can determine the nullclines and direction field of the system, simply by equating the pay-offs (see Appendix B). Thus, the rate of change of f_S will be zero when $Z_S = Z_{\bar{S}}$; the locus of this equality can be given as:

$$f_S = 1 - \frac{f_D(1 - f_D)}{(\frac{3}{4}i - 1) + f_D} \quad (11)$$

which describes the nullcline starting at ($f_D = 0; f_S = 1$), lying below $f_S = 1$ for $0 < f_D < 1$, and ending at ($f_D = 1; f_S = 1$). It is obvious that the male nullcline ends at ($f_D = 1; f_S = 1$): with all females being dependent, the \bar{S} -males having no \bar{D} -females to sustain their offspring. Slightly less obvious is why the nullcline begins at ($f_D = 0; f_S = 1$): When all females are independent, there are equal numbers of \bar{S} -males and of females not matched to S-males, implying $Z_{\bar{S}} = \frac{P_M}{2}$, which is smaller than Z_S whenever $f_S < 1$

(and $\gamma > 0$). Besides the nullcline described by equation (11), there are two trivial male nullclines, $f_S = 0$ and $f_S = 1$.

The female nullcline is found from $Z_D = Z_D^*$, and is given by:

$$f_S = \gamma \frac{1}{\beta_i - 1} + f_D \quad (12)$$

There are again two trivial nullclines, $f_D = 0$ and $f_D = 1$.

The intersections of male and female nullclines define equilibria. The stability of these equilibria can be assessed by consideration of the direction field, combined with the Routh-Hurwitz criteria for stability. As illustrated in Figure 2 below, three cases can be distinguished:

$$\text{I} : \beta_i < \beta_{i0} \stackrel{\text{def}}{=} \gamma + 1 \quad (13)$$

$$\text{II} : \beta_{i0} < \beta_i < \beta_{ihi} \stackrel{\text{def}}{=} \frac{1}{1 - \gamma} \quad (14)$$

$$\text{III} : \beta_i > \beta_{ihi} \quad (15)$$

In case I, the female nullcline described by equation (12) lies outside the state space $(0; 1) \times (0; 1)$. The single stable equilibrium is $(f_D = 0; f_S = 1)$: all females are independent, all males supportive. In case II, the female nullcline, equation (12), intersects the male nullcline, equation (11), in a stable equilibrium in which all four strategies are present. The point of intersection (f_D^*, f_S^*) depends on the parameters as follows:

$$f_D^* = \frac{1 + (1 - \beta_i \gamma) = \gamma}{1 + (1 - \beta_i \gamma) + \beta_i^2 \gamma (1 - \gamma)} \quad (16)$$

$$f_S^* = \frac{\gamma}{\beta_i - 1} + \frac{1 + \beta_i \gamma}{1 + (1 - \beta_i \gamma) + \beta_i^2 \gamma (1 - \gamma)} \quad (17)$$

In case III, the female nullcline, equation (12), lies below the male nullcline (11); the single stable equilibrium point is now $(f_D = 1; f_S = 1)$: the traditional role pattern.

The three cases depicted correspond to regions in the $\gamma - \beta_i$ parameter space of the model, separated by the loci of $\beta_i = \beta_{i0}$ and $\beta_i = \beta_{ihi}$ (Figure 2). For $\gamma = 1$, case III does not arise (β_{i0} lies at infinity). As β_i goes from β_{i0} to β_{ihi} for a given value of γ , the equilibrium point $(f_D^*; f_S^*)$ travels from $(0; 1)$ to $(1; 1)$. At some intermediate value β_i , f_S^* attains a minimum, and the proportion of \bar{S} -males is then at a maximum. This intermediate β_i value is

$$\beta_i = \frac{\gamma}{1 - \gamma} \quad (18)$$

Figure 2 shows $\bar{\alpha}$ as a dashed line. Let $(f_D^{\bar{\alpha}}; f_S^{\bar{\alpha}})$ denote the equilibrium point at this $\bar{\alpha}$ value. From equations (16), (17), and (18) it follows that

$$f_D^{\bar{\alpha}} = \frac{1}{2} \quad \text{and} \quad f_S^{\bar{\alpha}} = \frac{\gamma}{2} \left(\frac{p}{1+\gamma} + \frac{p}{1-\gamma} \right) : \quad (19)$$

Thus, the proportion of \bar{S} -males is maximal when there are equal numbers of D- and \bar{D} -females. This fraction $1 - f_S^{\bar{\alpha}}$ is in fact zero when $\gamma = 0$, as \bar{D} -females then become indistinguishable from D-females, and unable to support offspring of \bar{S} -males. When $\gamma = 1$, $1 - f_S^{\bar{\alpha}}$ becomes $1/2$ ($\bar{\alpha}$ lies at infinity). For intermediate values of γ , the \bar{S} -males fraction achieved at $\bar{\alpha}$ lies in between 0 and $1/2$. Prominent proportions of \bar{S} -males clearly require γ values near 1.

From this severe model we conclude that the traditional (D; S) pattern appears only when independent females are less able to generate earning power than males; if having offspring does not inhibit earning power, then female dependence will not spread through a population. (By construction, our severe model does not allow the required support of offspring to exceed maximal male parental support.) If, however, the effects of female sexiness are large relative to female earning power, outcomes correspond to the traditional role pattern of dependent females and supportive males. Mixed cases occur between these two extremes. It is interesting that the non-supportive male strategy persists only in the intermediate range II, where female earning power is relatively large. In some sense, this region perhaps represents a transition between the traditional society (with low γ and high $\bar{\alpha}$) to a modern hi-tech society (with high γ and low $\bar{\alpha} < \bar{\alpha}_{10}$). The parameters γ and $\bar{\alpha}$ characterize a community. Both can be estimated for modern human societies: γ is a fairly straightforward to estimate as the ratio of income awarded for comparable jobs between females and males. The following expression estimates $\bar{\alpha}$:

$$\bar{\alpha} = \frac{(1 - f_D)p}{(1 - p)f_D}$$

where f_D is the fraction of dependent females and p is the fraction of supportive males' earning invested in the offspring of dependent females. The former, f_D , is relatively easy to estimate (all that is required is a classification of females into dependent and independent, which can be done on the basis of self-reliance, that is, the presence of an independent income greater than some cut-off value), whereas the fraction p requires more detailed statistics which may be difficult to obtain in practice. It should be

interesting to correlate the β and $\frac{3}{4}$ values of a community with other socio-economic indices. For instance, technological advancement may correlate with high β values, while high β values may be found together with more stringent cultural mores governing 'appropriate' behavior in females (which bears upon perceived attractiveness).

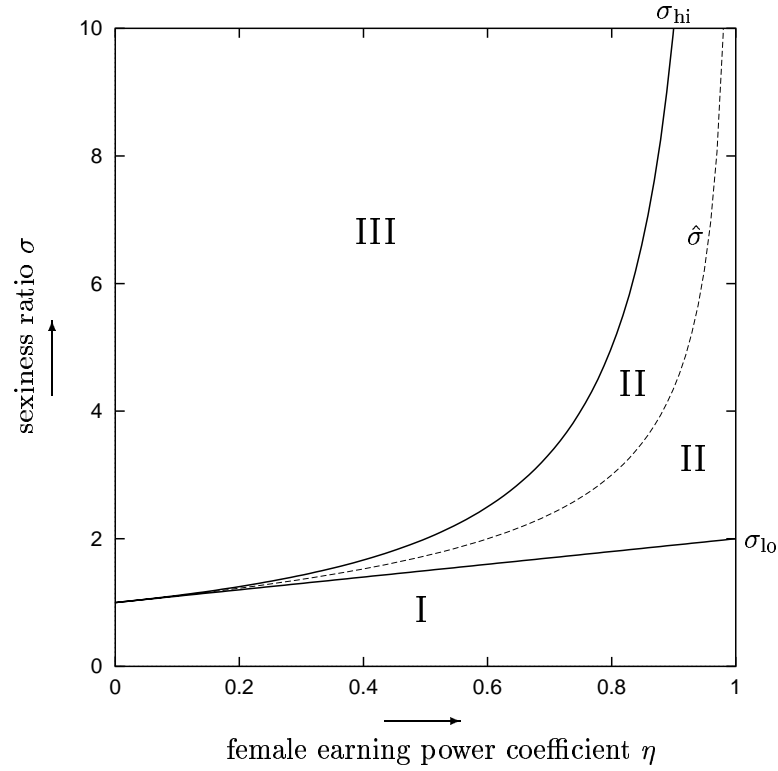


Figure 2: Nature of the equilibrium composition of the population as a function of female earning power and sexiness. Region I: all females independent, all males supportive; region II: all four strategies are present; region III: all females dependent, all males supportive. The proportion of non-supportive males is maximal on the line marked $\hat{\sigma}$.

4 Discussion

The following considerations suggest that male support is important in humans. The unique intelligence which characterizes the human 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, even though his hands can grasp tightly (but not tight enough to hold his own weight), a human baby cannot simply cling to his mother as she goes about her earning her living. Humans, relative to other primates, are born early; it is several years from birth before a human child can make his own way in the world. Human babies require constant care. The mother can benefit greatly from help in raising her offspring; male parental support may be crucial. In evolutionary time, females who are more successful at obtaining male parental support can have more surviving offspring; they will have a higher fitness than females who may be more able, in some respects, to raise their offspring alone but capture less male support in raising the offspring. Thus, when male parental care is important, evolution may favor females who are able to entice males to be faithful to the nest – that is, to provide support and care for the female and her offspring, although perhaps taking advantage of passing opportunities to mate, without commitment, with other females.

The central importance of female dependency in humans may be gleaned from the following two examples. The examples both illustrate that in hunter-gatherer societies, females and their offspring may be dependent on males. In one, females and their offspring are dependent on males for food sharing and in the other, for some food sharing and for protection from other males.¹²

Among the hunter-gatherer Ache Indians of Paraguay, who were virtually untouched by other civilizations until the nineteen sixties, male support of females through sharing of food appears crucial. Prior to the establishment of missions in Ache lands, most hunting was done by the males and most gathering, by the females. It is estimated that males contributed 82% of the caloric needs of the group. Females, of course, were not idle; they typically have their hands filled – literally and figuratively – with children. Kaplan and Robson (1999) present data on the amounts of food, measured in calories, consumed and produced by males, who hunt, and by females, who gather. Up until about age 45, perhaps when her youngest child is no

¹² Isaac (1978) has proposed that collective food sharing and processing approximately two million years ago was a critical step in the evolution of language, intelligence, and the sexual division of labor.

longer an infant, the typical Ache female does not support her own caloric needs. In contrast, a typical male in his prime will produce through hunting approximately double his own caloric requirements.¹³ In his prime as a hunter, at about age 33, he produces enough calories to feed himself and to provide the additional calories required by a female partner of child-bearing years and of two children, one aged 13 and the other aged 7.

Among the !Kung, who live in nomadic bands in the desert/savannah of southern Africa, the division of labor is strict: women gather, men hunt and children play – and men occasionally make war. Gatherers obtain about 60% of the food, and take less time to do their gathering than the hunters (who do, however, provide some essential nutrients). Interband ...ghts are rare but when they do occur and one side loses, the effects can be disastrous for the women and children of the defeated band.¹⁴ Indeed, it is apparent that the life style of the !Kung reduces the observed fertility of !Kung females. The evidence indicates that relative to !Kung women living their traditional nomadic life, women living nearer to cattleposts have more offspring. Indeed, it has been estimated that 52% of the nomadic !Kung females will bear no offspring. The ...gures for the Ache are quite different. In terms of a population growth model, of the sort in Robson and Wooders (1997) for example, the social norms governing the distribution of the gains from production of the Ache are more productive than those of the !Kung; populations grow faster when males contribute more parental support.

We have discussed 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. We have assumed that female ...tiness would benefit from expenditure of this surplus on parental investment, while male would benefit from expenditure on sexual competitiveness (body growth), insofar as females are able at all to raise offspring without support. In fact, depending on the female's power base, parental investment of this surplus may increase the ...tiness of both sexes. In particular, if females control male access to procreation, and are able to

¹³Michelle White suggests that this may be simply one solution to a coordination problem; the other solution would have females doing the hunting while males provided most of the gathered food and the child care. An obvious problem with this is that females have less upper body strength than males; it is the view of at least one of the authors of this paper that this lack of upper body strength is not entirely the result of lack of certain sorts of exercises. Male olympists and female olympists probably train equally hard but still the females appear to have less upper body strength. While we have argued that female dependency is a possible equilibrium outcome, we do not believe that the position of males and females are interchangeable.

¹⁴See Gould and Gould (1996), Hrdy (1981) and Landers (1992).

exact some sort of guarantee before allowing the male access, non-supportive males will not be ...t. On the other hand, if males are able to enforce sexual contact, investment in bodily strength confers ...tiness (both in combatting male rivals and perhaps in ensuring female cooperation).

The idea that females have evolved to be dependent in certain ways may explain that fact that females have less upper body strength than males and, because of this, are typically unable to defend themselves against attack by males, but it does not suggest that females are less able to function in the modern world of high tech and large social and economic organizations. In fact, the implication may be the opposite; because females had to evolve strategies to elicit male support and resolve conflicts with males and other problems in a nonviolent manner (in view of the male's greater physical strength), females may have evolved strategies that make them superior at various skills that are highly valued in modern societies.¹⁵

Intriguingly, cultural factors influence and modify the female power base on a time scale which is likely to be much faster than that of evolutionary dynamics. This disparity of time scales may result in our retention of instincts which evolved under circumstances that no longer prevail. We might do well to keep this in mind when we accord roles to men and women in generating economic power and in raising offspring.

5 Appendix A

We note some elementary properties of $f(x; \bar{x})$ which will be used below. First,

$$\frac{d}{dx} f(x; \bar{x}) > 0 \quad 0 < x < 1 \quad (20)$$

when $\bar{x} < \frac{1}{2}$, and, in addition,

$$\frac{d}{dx} f(x; \bar{x}) \begin{cases} > 0 & 0 < x < \frac{\bar{x}}{\frac{1}{2} + \bar{x}} \\ < 0 & x > \frac{\bar{x}}{\frac{1}{2} + \bar{x}} \end{cases} \quad (21)$$

¹⁵In fact, many evolutionary theorists and biologists take the view that human intelligence was an evolved outcome resulting from the demands of hunting. In summarizing this view, Hrdy writes "Success depended on special male skills: visual-spatial capacities, stamina, stalking abilities and especially cooperation." Hrdy (1989, p.5). In contrast, Hrdy (1989), in her own research, and Dunbar (1996), express viewpoints according a larger role in the development of intelligence to socializing behaviors.

when $\bar{x} > \bar{x}$.

To prove that equation (5) describes ES values, we consider the cases in turn.

Case 1: $\bar{x} > 1$. We take all non-mutant males at $x = \bar{x} = 1$. Since the mutant is present in a negligible fraction of the males, we can take $\bar{x} = \bar{x}$. By property (20) above, $f(1; 1) > f(x; 1)$ for any mutant with $x < \bar{x} = 1$, which is therefore unable to establish itself.

Case 2: $\bar{x} < 1$, $0 < \frac{1}{2} < \bar{x} < 1$. We take all non-mutant males at $x = \bar{x} = 1 - \frac{1}{2}$, and consider whether a mutant with $x \notin \bar{x}$ can invade, again with $\bar{x} = \bar{x}$. Since $\frac{1}{2} < 1 - \bar{x}$, $\bar{x} = 1 - \frac{1}{2} > \bar{x}$. We thus have $\bar{x} > \bar{x}$, and by property (21) above, a male can achieve maximal fitness for $x = \frac{\bar{x}}{\frac{1}{2} + \bar{x}} = \bar{x}$. Thus, no mutant $x \notin \bar{x}$ can achieve a strictly higher fitness than the population males at $\bar{x} = 1 - \frac{1}{2}$, and the population cannot be invaded by any such mutant.

Case 3: $\bar{x} < 1$, $\frac{1}{2} > 1 - \bar{x}$. In a population with $\bar{x} = \bar{x}$, all mutants such that $\frac{\bar{x}}{\frac{1}{2} + \bar{x}} < x < 1$ achieve the same maximal fitness $\frac{1}{\frac{1}{2} + \bar{x}}$ ($\bar{x} = \bar{x}$ is in that interval). Thus, mutants $x \notin \bar{x}$ can invade by drift. However, we can show that the population average \bar{x} returns to \bar{x} under such perturbations. If $\bar{x} < \bar{x}$, mutants with $x > \bar{x}$ have a higher fitness than males with $x = \bar{x}$, by property (20) above. As a result, \bar{x} increases. On the other hand, if $\bar{x} > \bar{x}$, property (21) implies $f(x; \bar{x}) > f(\bar{x}; \bar{x})$ for $\frac{\bar{x}}{\frac{1}{2} + \bar{x}} < x < \bar{x}$ and $x > \bar{x}$ since $x > \bar{x} > \frac{\bar{x}}{\frac{1}{2} + \bar{x}}$ (the latter is true because $\frac{1}{2} + \bar{x} > 1$, which itself follows from $\frac{1}{2} > 1 - \bar{x}$ and $\bar{x} > \bar{x}$). The population average \bar{x} will therefore decrease (conditional on the presence of mutants in the interval $[\frac{\bar{x}}{\frac{1}{2} + \bar{x}}; \bar{x})$). Since \bar{x} increases for $\bar{x} < \bar{x}$ and \bar{x} decreases for $\bar{x} > \bar{x}$, $\bar{x} = \bar{x}$ is ES. (Remark: the mild dependence on mutational drift may be taken as a reason not to regard this value as 'strictly' ES.)

6 Appendix B

We assume that the evolutionary dynamics of f_D and f_S are autonomous and only depend on the state $(f_D; f_S)$:

$$\begin{aligned} \frac{d}{dt} f_D &= H_D(f_D; f_S) \\ \frac{d}{dt} f_S &= H_S(f_D; f_S) \end{aligned} \quad (22)$$

The interpretation of the problem immediately tells us that

$$H_D = 0 \quad (f_D = 0 \text{ or } f_D = 1) \quad \text{and} \quad H_S = 0 \quad (f_S = 0 \text{ or } f_S = 1) \quad (23)$$

which define the nullclines on the boundaries of the phase space. For phase points in the interior of the phase space (that is $(f_D; f_S) \in (0; 1) \times (0; 1)$), we assume that H_D and H_S are smooth and, if the notion that the pay-offs govern the evolutionary dynamics is to make sense, the direction field should agree in sign with the differences in pay-offs:

$$H_D(f_D; f_S) \geq 0 \text{ as } Z_D \geq Z_D^* \text{ and } H_S(f_D; f_S) \geq 0 \text{ as } Z_S \geq Z_S^* : (24)$$

Stability of an equilibrium point on the boundary of phase space requires that this point is approached locally by at least one phase path on which the component of the tangent vector perpendicular to the boundary is directed towards the boundary (or, when the equilibrium point is in a corner, when the two components perpendicular to the boundaries are both directed towards the boundaries). The existence of such a path can be ruled out if all interior elements of the direction field in a neighborhood of the equilibrium have a perpendicular component away from the boundary; in that case the boundary is repulsive. This repulsiveness renders almost all boundary equilibria unstable, with the exception of the equilibrium at $(0; 1)$ which is stable for $\frac{3}{4} < \frac{3}{4}_{lo}$, and the equilibrium at $(1; 1)$ which is stable for $\frac{3}{4} > \frac{3}{4}_{hi}$.

Let \tilde{z} denote a perturbation of the $f_D; f_S$ system about the equilibrium point in the interior of the phase space. Expanding the components of the tangent vector to lowest significant order, we obtain the linearized system $\dot{\tilde{z}} = J \tilde{z}$ which is stable when the eigenvalues of the Jacobian J both have a negative real part, which is the case if and only if both the trace of J is negative and the determinant of J is positive. The first of these conditions is satisfied in virtue of assumption (24), whereas the second can be rendered as a condition on the slopes of the nullclines, which is readily verified by inspection.

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