

”The Evolutionary Origins of Beauty Preferences: Endogamy and Pre-Historic Marriage  
Markets”

Leanna Mitchell

February 27, 2014

Working Paper

Abstract: This paper models information about potential spouses in the pre-Holocene marriage market. I assume that agents have better information about the quality of potential spouses from their own group than they do about those from other groups. In the absence of aversion to endogamy, I show that the exogamous marriage market breaks down completely. Repeated endogamy over many generations then results in severe fitness depression. A mutation for aversion to endogamy would be very beneficial in this situation. Such a mutation would spread, eventually resulting in a lower steady-state population-wide level of fitness depression. Introducing an additional mutation, for the capacity to credibly signal quality, decreases the level of fitness depression still further. Physical examples of credible signals of quality include the capacity of both sexes to grow long head hair, and for females to grow large breasts.

# 1 Introduction

Humans of both sexes have long head hair, and females have breasts that are, on average, many times larger than those of other primates, despite serving the same function. Modern humans in all societies display strong preferences over these features when choosing mates, despite the fact that in many societies they are only weakly correlated with fertility. People also spend significant resources on enhancing these features.

A second, seemingly unrelated puzzle, is that many mammals, including humans, avoid mating with close relatives[17]. Furthermore, humans seem averse to mating close childhood acquaintances, even when unrelated[18]. This paper hypothesizes that reduced fitness due to inbreeding depression was a significant problem for early humans, and that both beauty features and aversion to endogamy arose via evolution by natural selection because they increased both individual and group fitness. In particular, there was likely an asymmetric information problem in the pre-Pleistocene exogamous marriage market, which these traits ameliorated.

Inbreeding avoidance and sexual selection are traditionally addressed separately and in the biological literature, but since they can best be explained via the economics of a marriage market, and because they have important implications for human preferences, this paper belongs in the economics literature. Modern humans spend a significant fraction of their income attempting to enhance their head hair, beards and breasts, and a significant fraction of their attention observing these traits in others. Such preferences have persisted even in societies where sickness and starvation are rare, and where there are stronger observable signals of mate quality, such as income and age, as well as in a declining interest in fertility as a result of the demographic transition.

This paper develops a model of information and spousal choice in the pre-Holocene marriage market. It is impossible to directly observe institutions that existed more than 12 000 years ago, but it is possible to infer from the archaeological evidence and institutions of recent low-density hunter gatherers that the following stylized facts were generally true. Relative to other animals, humans are monogamous and both parents invest highly in each offspring [8]. For these reasons,

mate choice for both sexes is extremely important. Relative to modern times, population density was extremely low, so there would have been relatively few candidates for marriage in a given geographic area.

From at least 200 000 years ago when human ancestors became anatomically modern, until 13 000 years ago when the holocene began, social organization is hypothesized to have consisted of informal, autonomous groups of approximately fifteen to twenty individuals , often including a mated pair, some of their children and the spouses of those children, and grandchildren. Groups were likely fluid, with nuclear families alternating between living with members of paternal and maternal extended families.

Exogamous marriage can be beneficial in that it reduces risk by increasing access to a greater variety of socially controlled resources, it helps secure political alliance for conflict, and searching exogamously increases the pool of potential mates. In a sparsely populated foraging society, however, all of these benefits are minimized, and so such societies are likely to have to relatively high levels of endogamy.

Endogamy increases the relatedness of both parents and offspring to other members of the group. Relatives will, in general, have a higher coefficient of relatedness to the offspring of an endogamous marriage than those of an exogamous marriage. As a result, higher levels of altruism can be maintained in equilibrium[5]. Inbreeding can thereby reduce inefficiencies due to situations involving prisoner's dilemma and moral hazard problems, which gives the individuals and groups involved an evolutionary advantage.

An important contribution of this paper is to expose an additional incentive to marry endogamously: asymmetric information over mate quality. In small foraging societies, individuals have many opportunities to observe the quality of potential mates within their own group. Important traits such as foraging ability, social skills and recent disease history would be well known within the group. The quality of potential mates from other groups, however, would not be directly observable. Family groups in mobile foraging societies are almost always part of a regional social network[12], but they spend much less time with individuals from these other groups, perhaps only a few days per year. They therefore have fewer opportunities to directly observe the quality

of potential mates from other groups. In the simplistic scenario where nuclear families alternate between living with the paternal and maternal extended families, children would never live with any other children who are related more distantly than first cousin. As a result, the exogamous marriage market would suffer asymmetric information problems similar to Akerlof's 'Market for "Lemons"'[1].

It is well known to biologists and economists that consanguinity generally results in offspring with higher death rates and poorer health. This reduced fitness is called inbreeding depression. Repeated consanguinity in generations of a family, furthermore, increases the . Family history is not immediately observable to an individual, so it is difficult for her to assess the fitness costs of a further consanguineous marriage. In the model, aversion to endogamy is subject to natural selection and will adjust to changes in the frequency of endogamy.

An additional question is, why do both human sexes display exaggerated beauty features? Humans are not alone in displaying costly signals of quality. Other animal species, for example peacocks and sea lions, display traits that are credible signals of quality. In polygamous species, these traits are restricted to sexes which invest very little in the offspring, and the traits tend to be extremely costly[8]. The plumage of male peacocks is costly to produce and makes them significantly more vulnerable to predators . Human secondary sexual characteristics are unusual in that females as well as males display such traits, and that they seem relatively inexpensive.

Human beauty traits credibly signal quality, thereby improving information in the marriage market. Furthermore, preferences that accurately reflect the information expressed by such traits would be selected for in the opposite sex[13]. Theory from Spence's signaling model is used here[19], with the modification that the type space and possible signals are continuous. For the purposes of this paper, human beauty features are secondary sexual characteristics in the traditional biological sense: genetically controlled traits or behavior that are more extensively displayed by higher quality individuals, and which exerts a caloric cost .

This paper shows that early humans likely faced an inbreeding problem, due to a breakdown in the exogamous marriage market. Under these conditions, aversion to endogamy and displaying and interpreting costly signals of quality enhance individual fitness. Furthermore, the emergence

of such traits in a population would at least partially solve the inbreeding problem, thereby also increasing group fitness. Thus, both individual and group selection would promote the spread of the traits.

The paper proceeds as follows. In Section 2, I review the relevant economic and biological literature. In Section 3, I model the marriage market and then state some benchmark results, assuming no aversion to inbreeding. Section 4 introduces aversion to inbreeding and shows that asymmetric information still causes a significant amount of fitness depression. 5 introduces an incentive compatible signal. 6 shows that for a uniform distribution of quality, a population with signaling would have less fitness depression due to inbreeding than a non-signaling population, and concludes

## 2 Literature Review

There are many relevant literatures. I briefly review here the most relevant aspects of the following literatures: modern expenditures on enhancing beauty, the labour market value of beauty, marriage market matching, endogamy vs exogamy, inbreeding and fitness depression, human consanguinity, group-mate aversion, the economic literature on signaling, the biological literature on signaling, and the physiology of human beauty traits.

### Marriage Market

Mike Peters analyzes matching games in which both players are 'buyers' and 'sellers' simultaneously in 'The premarital Investment Game' [16]. High quality and low quality agents make investments to enhance their quality, assuming that they will be matched assortatively on the market in a later period. continuous. Stable equilibria and equilibrium selection rules are analyzed separately by Cho and Kreps[7] and Banks and Sobel[2], both in 1987.

According to Shapley, for any marriage market with  $n$  women and  $n$  men, and any set of preferences, there is a stable set of marriages. Assuming that all individuals have the same preferences, increasing in  $\theta$ , and this gives a unique stable set, with the highest quality woman marrying the

highest quality man, and so forth. If the

### **Endogamy vs Exogamy Incentives**

There are several established reasons why endogamy can be attractive. Endogamy (marrying within group), is attractive to individuals because it increases their offsprings' genetic relatedness to other adults. Close genetic relatedness has the benefit that it promotes altruism due to Hamilton's rule of kin selection, [10], [11], and therefore greater individual fitness. Exogamously married couples would have to choose a group to live with, and their children would be less related to the adults in that group than the other children, putting them at a disadvantage.

The main theoretical incentives for humans to marry exogamously are i) increase mobility ii) attain political alliance and iii) access a larger pool of potential mates, in hopes of getting a better match. The first reason is perhaps the most important. Marrying exogamously provides the family with a choice regarding which extended family to live with, and when families control access to land, this means access to a larger and more varied land area. In a sparsely populated nomadic foraging economy, however, property rights are virtually non-existent. There is virtually no evidence of the existence of property rights to land, and economic theory predicts there wouldn't be.

The second reason for exogamous marriage is to form alliances for purposes of defense and attack. In low density foraging economies, however, land is open access and organized warfare is very uncommon. The third reason involves matching theory and the pool of potential mates. The larger the pool, the more likely it is that an individual finds a 'good' match. Suppose the pool of potential mates involves all opposite sex, fertile individuals within a 200 km radius of current location. The lower population density is, the larger percentage of these potential mates will be within one's own group. Another way to say this is that the lower the population density, the higher are the search costs of finding an exogamous partner.

Ignoring fitness depression, endogamy is attractive because it increases the relatedness of one's offspring to non-parent members of the group. In accordance with Hamilton's rule, non-parent relatives will have the highest coefficient of relatedness to children when they are the offspring of an endogamous marriage. Very high levels of altruism can result. Furthermore, there is theoretical

evidence that equilibrium levels of altruism are increasing in measures of inbreeding. Inbreeding can thereby reduce inefficiencies due to situations involving prisoner's dilemma or moral hazard problems.

### **Inbreeding**

Lower fitness in the offspring of consanguineous parents is due to a higher frequency of homozygosity in offspring. This frequency,  $f$  is known to biologists as Wright's coefficient, and the same statistic can be used to refer to the relatedness of the parents of a given offspring. Offspring of parents with higher relatedness coefficient have a systematically larger fraction of pairs of genes that are homozygous. Homozygosity in itself does not decrease fitness, but it tends to increase the percentage of loci in an individual at which both alleles are dysfunctional. If both alleles at a loci are dysfunctional, the products of those genes are defective. A second derivation of relatedness coefficients finds that the same parameter  $f$  also measures homozygosity of an offspring, relative to the level of homozygosity in the population as a whole .

For example, cousins who are otherwise completely outbred has a Hamiltonian coefficient of  $R = 1/8$ , but double first cousins have  $R = \frac{1}{4}$ . Much more complicated relationships, such as single first double second cousinship are possible. For this reason, and because of uncertain paternity, the degree of relatedness relevant for evaluating the fitness costs of consanguinity is not observable to an individual.

Marrying a relative, however, results in genetic problems due to homozygous recessive genes[6]. Offspring are more likely to inherit two copies of a defective gene, decreasing their fitness. Repeated inbreeding further increases the homozygotic frequency, Wright's coefficient, which is the probability that a pair of alleles in any individual at a random locus are identical by descent. Repeated inbreeding is additionally detrimental in that it decreases genetic variation within a population, making it less adaptable to changing environmental conditions (cite).

### **Human Consanguinity**

In humans, the offspring of first cousin parents are on average 3 cm shorter[?], 4-5 times as likely to be mentally retarded, and 2.5 times as likely to have physical malformations at the time of birth, compared to the offspring of parents who are not close relatives.

## **Signaling in Economics and Biology**

The economic and biological signaling literatures study similar problems, with somewhat different foci. The economics literature investigates the choices of utility maximizing agents, given an exogenous environment featuring asymmetric information and signaling. The biological literature takes a more evolutionary approach, and discusses how certain behavior, physical structures and preferences may arise as a result of evolution by natural selection. This paper incorporates aspects of both literatures, focusing specifically on the literature relevant to the marriage markets of early humans.

### **Signaling - Economics**

The economic literature on asymmetric information and costly signaling begins with Akerloff's 'The Market for "Lemons"[1] in 1970 and Spence's "Job Market Signaling,"[19] in 1973. These papers are not summarized here as they are well known to economists. Only features that are not controlled by genes and are physically evident in people of all ethnicities are considered. Although preferences for costly adornment may have closely related evolutionary origins[13], such things as makeup, clothing, hair styling, tattoos, piercings and tanning are not considered beauty traits for the purposes of this paper.

### **Signaling - Biology**

The relevant biological literature on signaling began in 1975 with "Mate Selection-A Selection for a Handicap" by Zahavi[21]. In this paper, Zahavi develops a theory that "handicaps" can develop through mate selection. Prior to 1975, biologists had tried to explain the evolution of traits such as bright colors on birds and antlers on deer using complicated models of kin selection and group selection. Zahavi suggested that such traits were selected for because the opposite sex used them as a test of quality. Zahavi seems to have developed the idea independently of Spence, as he cites only biological works. In 1990 Grafen developed a mathematical model of biological signaling, and showed that if the handicap principles developed by Zahavi are met, an evolutionarily stable signaling equilibrium exists, and furthermore that any evolutionarily stable equilibrium satisfies the handicap principles[9]. Grafen is familiar with the economic literature, discussing the contribution of papers by Spence, Cho, and Banks, among others. Perhaps the most



relevant paper to this one is “Separating Equilibria in Continuous Signaling Games” by Bergstrom, Számádó and Lachmann[4]. Bergstrom et al. analyze the role of the cost function in a signaling game, and show that the equilibrium cost for an individual of quality  $q$  can be arbitrarily cheap, while still supporting a fully separating equilibria.

### Physiology

Some examples of beauty traits in humans include long thick head hair in both sexes, large breasts[14] and smooth skin in females, and beards in males[3], as well as many other possible traits[3]. These traits are less evident in individuals who have recently suffered poor nutrition, disease, or are simply older. Head hair, for example, becomes duller, thinner and falls out with progressively worse nutrition, disease or age[20]. Healthy human breasts are much larger than those of other healthy primates[14], despite having the same function. These traits are costly to maintain, but none of them seem to increase probability of death very significantly or require a large percentage of of daily consumed calories to maintain.

This paper pulls together elements of these literatures to explain the evolution of some deeply rooted aspects of human behavior.

## 3 Environment

### 3.1 The Matching Game

Time is discrete and there is a continuum of groups. In each period, each group  $i$  has one marriage market candidate  $i_t$ , and is randomly matched with another group,  $j$ , who has one marriage market candidate,  $j_t$ . Candidates  $i_t$  and  $j_t$  decide simultaneously whether they wish to marry one another or to marry within their own group.  $y_t^i \in Y = \{0, 1\}$ , where  $y_t^i = 1$  denotes a choice of exogamy and  $y_t^i = 0$  a choice of endogamy;  $y_t = (y_t^i, y_t^j)$  is the vector of choices in period  $t$ . An exogamous marriage occurs in period  $t$  if and only if  $y_t = (1, 1)$ , that is, if and only if both candidates choose it.

Candidate  $i_t$  is endowed with quality  $\theta_t^i \in \Theta = [0, \infty)$ . Qualities are independent draws from an identical distribution with cumulative distribution function  $F(\theta)$ .  $F(\theta)$  is common knowl-

edge, twice continuously differentiable and strictly increasing on interior values of its domain. Furthermore  $F(0) = 0$  and  $f(\theta) > 0$ .

If an agent marries within her group, she receives a partner who is equal to her own quality, with certainty.

### 3.2 Fitness Depression

Denote by  $\delta^t \in \Delta = [0, 1]$  the coefficient of fitness depression due to an endogamous marriage.  $\delta^t$  is constant across a society in a given period, and not observed by any of the agents.

Each mated pair has one offspring. The offspring survives to adulthood with probability:

$$P_s = \left\{ \begin{array}{ll} G(\theta_m, \theta_f) & \text{iff } y = (1, 1) \\ (1 - \delta_t) G(\theta_m, \theta_f) & \text{iff } y \neq (1, 1) \end{array} \right\} \quad (1)$$

Where  $\theta_m$  denotes the quality of the mother and  $\theta_f$  the quality of the father.

Assume that each partial derivative of  $G$  is positive and constant in partner's quality. Thus  $G_1(\theta_m, \theta_f)$  is positive and constant in  $\theta_f$ .  $G_2(\theta_m, \theta_f) > 0$  and constant in  $\theta_m$ .

### 3.3 Preferences and Evolution

Since agents cannot directly observe  $\delta^t$ , suppose initially that their objective function is simply  $G(\theta_i, \cdot)$ . An agent  $i$  therefore has the following objective function:

$$U_i = \left\{ \begin{array}{ll} \theta_j & \text{iff } y = (1, 1) \\ \theta_i & \text{iff } y \neq (1, 1) \end{array} \right\} \quad (2)$$

If the agent marries exogenously she receives utility equal to quality of her partner,  $\theta_j$ . If she marries endogamously, her utility is  $\theta_i$ . Each agent  $i$  wants to choose  $y_i = 1$  if and only if  $\theta_j$  is higher than  $\theta_i$ . Since  $i$  is risk neutral, this corresponds to iff:

$$E[\theta_j | y_j = 1] > \theta_i \quad (3)$$

**Proposition 1.** *The unique Bayesian Nash Equilibrium of the game  $H(0)$  is:  $\sigma_i(\theta_i, 0) = 0$  and  $\sigma(\theta_j, 0) = 0$ .*

*Proof.*  $i$  has a prior over the expected quality of  $j$  given  $y_j = 1$ :  $E(\theta_j | y_j = 1)$ . The following strategy is dominant ex ante:  $\sigma(\theta_i) = 1$  if and only if  $E(\theta_j | y_j = 1) \geq \theta_i$ . In the case that agent  $j$  chooses  $y_j = 1$ , agent  $i$  is strictly better off in expectation given this strategy. If agent  $j$  chooses  $y_j = 0$ , all strategies are equivalent. Expected utility of marrying exogamously is constant in own quality, while expected utility of marrying endogamously is increasing in own quality. Any strategy that is not a cutoff rule is strictly dominated ex-ante by the strategy  $y_i = 1$  iff  $\theta_i < \bar{\theta}$  for some  $\bar{\theta} \in \Theta$ . Since the problem is perfectly symmetric,  $\bar{\theta}_i = \bar{\theta}_j = \bar{\theta}$ . At the cutoff quality, an agent is indifferent, so  $\bar{\theta}$  must solve  $\frac{\int_0^{\bar{\theta}} x f(x) d(x)}{F(\bar{\theta})} = \bar{\theta}$ . Denote such a solution as  $\bar{\theta}_e$ . The only solution is  $\bar{\theta}_e = 0$ . Thus, the market unravels completely and  $y_t = (0, 0)$  with probability 1.  $\square$

The intuition for this result comes directly from Akerlof's Market for Lemons, where the market collapses from the top until only the lowest quality goods remain. Since the measure of individuals with quality zero is zero, no exogamous marriages occur in equilibrium.  $i$  and  $j$  will choose endocamy regardless of their own quality.

### 3.4 Dynamics

The inbreeding coefficient for a particular group  $i$ ,  $\delta^i$ , is a Markov state variable, with transition function:

$$1 - \delta_{t+1}^i(y_t) = \left\{ \begin{array}{ll} 1 & \text{if } y_t = (1, 1) \text{ and } 1 - \delta_t^i + \epsilon > 1 \\ 1 - \delta_t^i + \epsilon & \text{if } y_t = (1, 1) \text{ and } 1 - \delta_t^i + \epsilon \leq 1 \\ 1 - \delta_t^i - \epsilon & \text{if } y_t \neq (1, 1) \text{ and } 1 - \delta_t^i - \epsilon > 0 \\ 0 & \text{if } y_t \neq (1, 1) \text{ and } 1 - \delta_t^i - \epsilon \leq 0 \end{array} \right\} \quad (4)$$

where  $\epsilon$  is a small positive number, and  $\delta_{t+1}^i$  is the realization of  $\delta$  in the next period.

If the marriage of group  $i$  in period  $t$  is exogamous,  $\delta^i$  decreases by a small amount. If it is endogamous,  $\delta^i$  increases by a small amount.

**Corollary 1.** *Suppose that all agents in a society have preferences as in 2. From any initial set of  $\delta_0^i$ , all fitness depressing coefficients will converge directly to  $\delta = 1$ , and then remain within the interval  $[1 - \epsilon, 1]$ .*

*Proof.* From 1 the only BNE is where  $y = (0, 0)$ . Therefore, for all  $1 - \delta_t > 0$ ,  $1 - \delta_{t+1} =$   

$$\left\{ \begin{array}{ll} 1 - \delta_t - \epsilon & \text{if } 1 - \delta_t - \epsilon > 0 \\ 0 & \text{if } 1 - \delta_t - \epsilon \leq 0 \end{array} \right\}. \quad \square$$

## 4 Aversion to Endogamy

In this section individuals still cannot observe  $\delta^t$ , but suppose nature can endow them with preferences regarding endogamy vs exogamy. Specifically, they discount endogamy by some factor  $1 - \lambda \in [0, 1]$ . This discount factor is heritable; suppose that an offspring inherits its father's preferences with probability  $\frac{1}{2}$  and its mother's with probability  $\frac{1}{2}$ .

Over many generations, nature observes the value of  $\delta$  in the population, and endows agents with preferences that ensure they maximize expected offspring.

Assume that all individuals in period  $t$  are averse to endogamy by a factor of  $1 - \lambda_t \in [0, 1]$ . Utility is therefore equal to the discounted quality of one's partner, as follows:

$$U_i^t = \left\{ \begin{array}{ll} \theta_t^j & \text{iff } y = (1, 1) \\ (1 - \lambda^t) \theta_t^i & \text{iff } y \neq (1, 1) \end{array} \right\} \quad (5)$$

The next proposition is a generalization of 1.

In the resulting game,  $H(\lambda_t)$ , a strategy is a function  $\sigma : \Theta \times \Lambda \rightarrow Y$  that satisfies  $\sigma(\theta_t^i, \lambda_t) \in \{0, 1\}$ .

**Proposition 2.** *A set of strategies  $\sigma_i(\theta_i, \delta)$ ,  $\sigma_j(\theta_j, \delta)$  is a Bayesian Nash Equilibrium of the game  $H(\lambda)$  iff:*

$$\sigma_i(\theta_i, \lambda) = 1 \Leftrightarrow \theta_i < \bar{\theta}_e$$

$$\sigma_j(\theta_j, \lambda) = 1 \Leftrightarrow \theta_j < \bar{\theta}_e$$

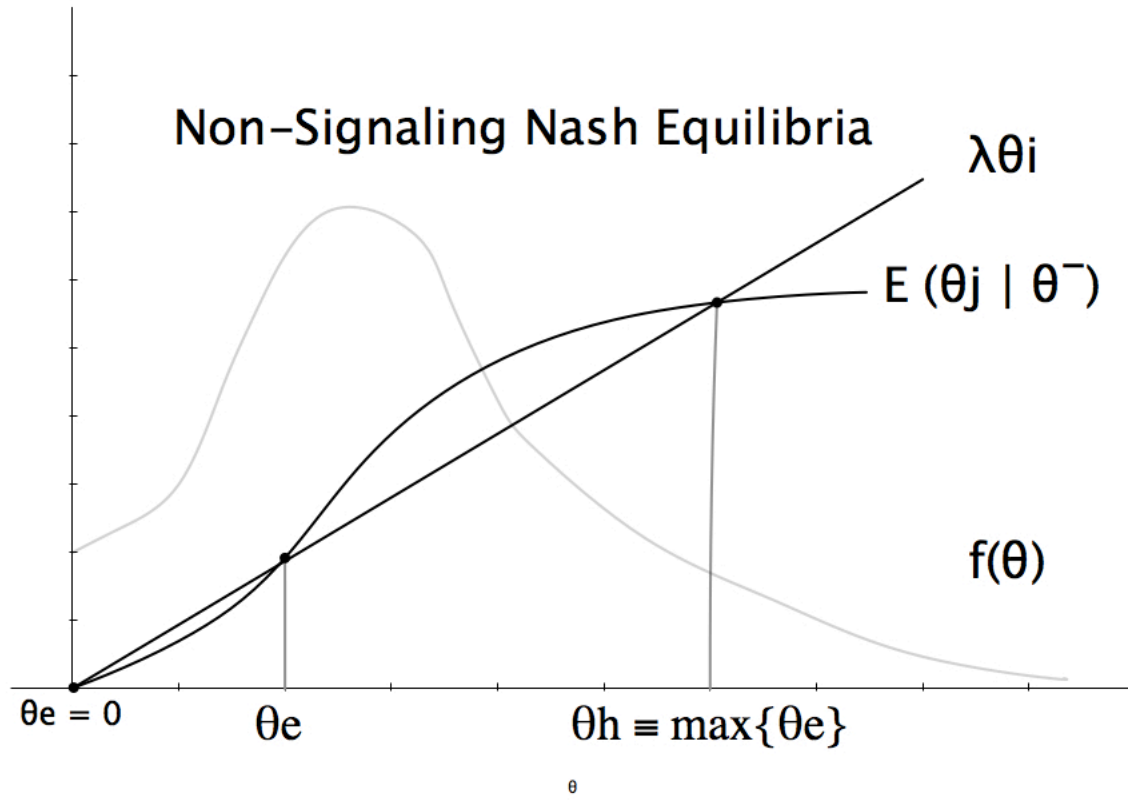
where  $\bar{\theta}_e$  is a solution to:

$$\frac{\int_0^{\bar{\theta}} x f(x) d(x)}{F(\bar{\theta})} = (1 - \lambda_t) \bar{\theta} \quad (6)$$

*Proof.* As in the benchmark model, any strategy that is not a cutoff rule is strictly dominated ex-ante by the strategy  $y_i = 1$  iff  $\theta_i < \bar{\theta}(\lambda_t)$  for some  $\bar{\theta}(\lambda_t) \in \Theta$ . Since the problem is perfectly symmetric,  $\bar{\theta}_i = \bar{\theta}_j = \bar{\theta}$ . At the cutoff quality, an agent is indifferent, so  $\bar{\theta}_e$  must solve:  $\frac{\int_0^{\bar{\theta}} x f(x) d(x)}{F(\bar{\theta})} = (1 - \lambda_t) \bar{\theta}$ .  $\square$

**Corollary 2.**  $\bar{\theta}_e = 0$  is a BNE for any  $\lambda_t$

The value of  $\lambda_t$  determines the set of Nash equilibria,  $\{\bar{\theta}_t^e\}$ . There may be multiple Bayesian Nash equilibria, as illustrated in the following graph:



I now introduce an equilibrium selection criterion, based on the principle of group selection.

**Definition 1.**  $\theta_t^h \equiv \max\{\bar{\theta}_t^e\}$

If there exists more than one  $\bar{\theta}_t^e$  for a given  $\lambda$ , the society co-ordinates on the highest one,

$\theta_h \equiv \max \{\bar{\theta}_t^e\}$ . This assumption relies on a fairly weak application of the principle of group selection. That is, populations who co-ordinate on  $\max \{\bar{\theta}_t^e\}$  can support more exogamy than those who co-ordinate on lower values of  $\bar{\theta}_t^e$ . Populations with higher rates of exogamy will produce offspring with higher mean fitness than those who cannot, and will replace the inferior populations via evolution by natural selection.

Note that for high enough  $1 - \lambda_t$ ,  $\theta_t^h = 0$ . In this case, all candidates will choose endogamy.

## 4.1 Mutant Invasion

Consider a population of individuals with the same degree of aversion to endogamy,  $\lambda \in [0, 1]$ . Suppose that a mutation occurs: one individual has a different degree of aversion:  $\lambda'$ . The incumbent degree of aversion  $\lambda$  is *evolutionarily stable against*  $\lambda'$  if an individual carrying the incumbent degree of aversion obtains, on average, a higher fitness than an individual carrying the mutant degree. The incumbent degree  $\lambda$  is *evolutionarily stable* if this holds for every  $\lambda' \neq \lambda$ .

**Proposition 3.** *The aversion factor  $1 - \lambda_t$  is evolutionarily stable if and only if  $\lambda_t$  is equal to  $\delta_t$ .*

*Proof.* Fitness maximizing preferences are those that maximize the net value of partner:

$$U_i = \left\{ \begin{array}{ll} \theta_j & \text{iff } y = (1, 1) \\ (1 - \delta) \theta_i & \text{iff } y \neq (1, 1) \end{array} \right\} \quad (7)$$

□

Assume from now on that  $\lambda$  adjusts immediately to any changes in  $\delta$ . That is, all agents maximize expected surviving offspring and therefore have the preferences in 7.

## 4.2 Dynamic Results

In preparation for the dynamic analysis, I first calculate the probability that both candidates draw qualities below  $\theta_h(\delta)$ , and therefore both choose exogamy. The probability that candidate  $i$  chooses exogamy is simply  $F(\theta_h(\delta))$ , the cumulative distribution function evaluated at  $\theta_h(\delta)$ .

Since quality draws are independent, the probability that they both choose exogamy is just this integral squared:

**Lemma 1.** *After  $\delta$  is realized but before  $\theta_i, \theta_j$  are realized, the probability of an exogamous marriage is  $p(y = (1, 1) | \delta) = [F(\theta_h(\delta))]^2$ .*

I now turn to the long run behavior of  $\delta_t$ . From 4:

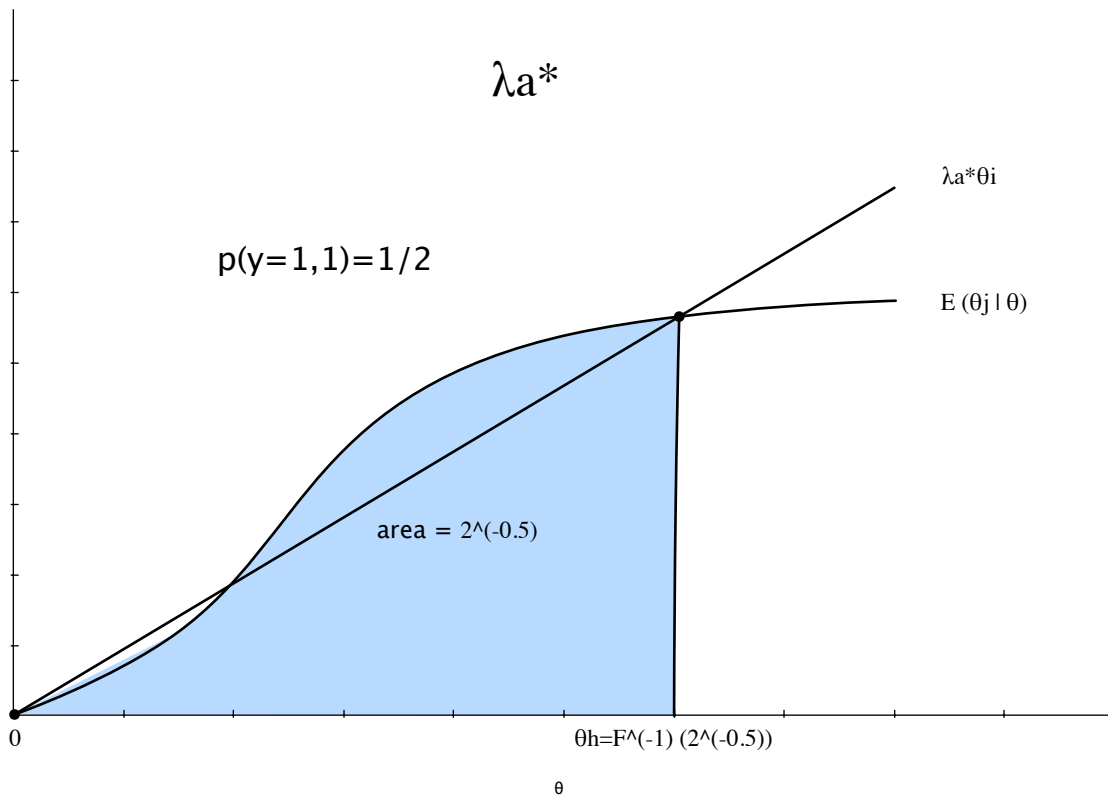
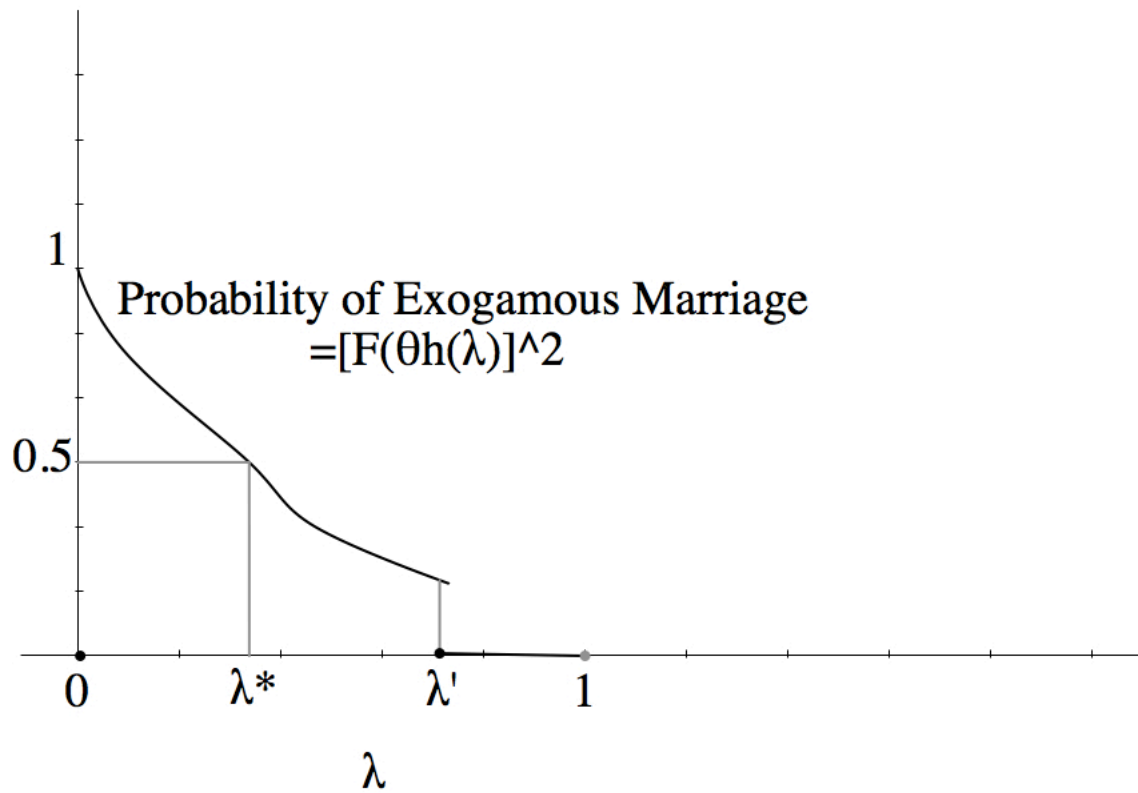
$$1 - \delta_{t+1} = \begin{cases} 1 & \text{if } y = (1, 1) \text{ and } 1 - \delta_t + \epsilon > 1 \\ 1 - \delta_t + \epsilon & \text{if } y = (1, 1) \text{ and } 1 - \delta_t + \epsilon \leq 1 \\ 1 - \delta_t - \epsilon & \text{if } y \neq (1, 1) \text{ and } 1 - \delta_t - \epsilon > 0 \\ 0 & \text{if } y \neq (1, 1) \text{ and } 1 - \delta_t - \epsilon \leq 0 \end{cases}$$

**Lemma 2.** *For all  $1 - \delta \in [0, 1 - \delta']$ , the probability of exogamous marriage is strictly decreasing in  $1 - \delta$ . Furthermore,  $p[(y = 1, 1) | 1 - \delta = 0] = 1$ , and  $p[(y = 1, 1) | 1 - \delta > 1 - \delta'] \simeq 0$ . There exists  $1 - \delta \in (0, 1 - \delta')$  such that  $p(y = 1, 1) = \frac{1}{2}$ .*

*Proof.* Since the probability of exogamous marriage decreases continuously on the interval from  $[0, 1 - \delta']$ , and this probability is 1 at  $1 - \delta = 0$  and 0 at  $1 - \delta > 1 - \delta'$ , there must exist  $1 - \delta \in (0, 1 - \delta')$  such that the probability of exogamous marriage is  $\frac{1}{2}$ .  $\square$

**Lemma 3.** *In equilibrium, the probability of exogamy is arbitrarily close to  $1/2$ .  $\theta_h^* = F^{-1}(1/\sqrt{2})$ .*

*Proof.* The probability of exogamous marriage is strictly decreasing in  $\delta$ , so the system has negative feedback. After sufficiently many periods and for arbitrarily small  $\epsilon$ , the probability of exogamous marriage will be arbitrarily close to  $\frac{1}{2}$ . From 1 the probability of exogamy is  $p(y = (1, 1) | \delta) = [F(\theta_h(\delta))]^2$ . Equilibrium fitness depression occurs when probability of exogamy is  $1/2$ . This gives  $[F(\theta_h^*(\delta))]^2 = \frac{1}{2}$ , which implies that  $\theta_h^* = F^{-1}(1/\sqrt{2})$ .  $\square$



**Proposition 4.** From any initial conditions  $\{\delta_i^0\}_i$ ,  $1 - \delta$  converges to:



$$1 - \delta_a^* = \frac{\sqrt{2} \int_0^{F^{-1}(1/\sqrt{2})} x dF(x)}{F^{-1}(1/\sqrt{2})} \quad (8)$$

*Proof.* From 6 and 4.1,  $\frac{\int_0^{1-\delta_h^*} x dF(x)}{F(1-\delta_h^*)} = (1 - \delta^*) \theta_h^*$  and from 3  $\theta_h^* = F^{-1}(1/\sqrt{2})$ .  $1 - \delta^*$  is therefore equal to:  $1 - \delta_a^* = \frac{\sqrt{2} \int_0^{F^{-1}(1/\sqrt{2})} x dF(x)}{F^{-1}(1/\sqrt{2})}$ . There is only one possible solution to this equation, so  $\delta^*$  is unique. □

## 5 Aversion to Group Mates and Signaling

### 5.1 Utility and the Agent's problem

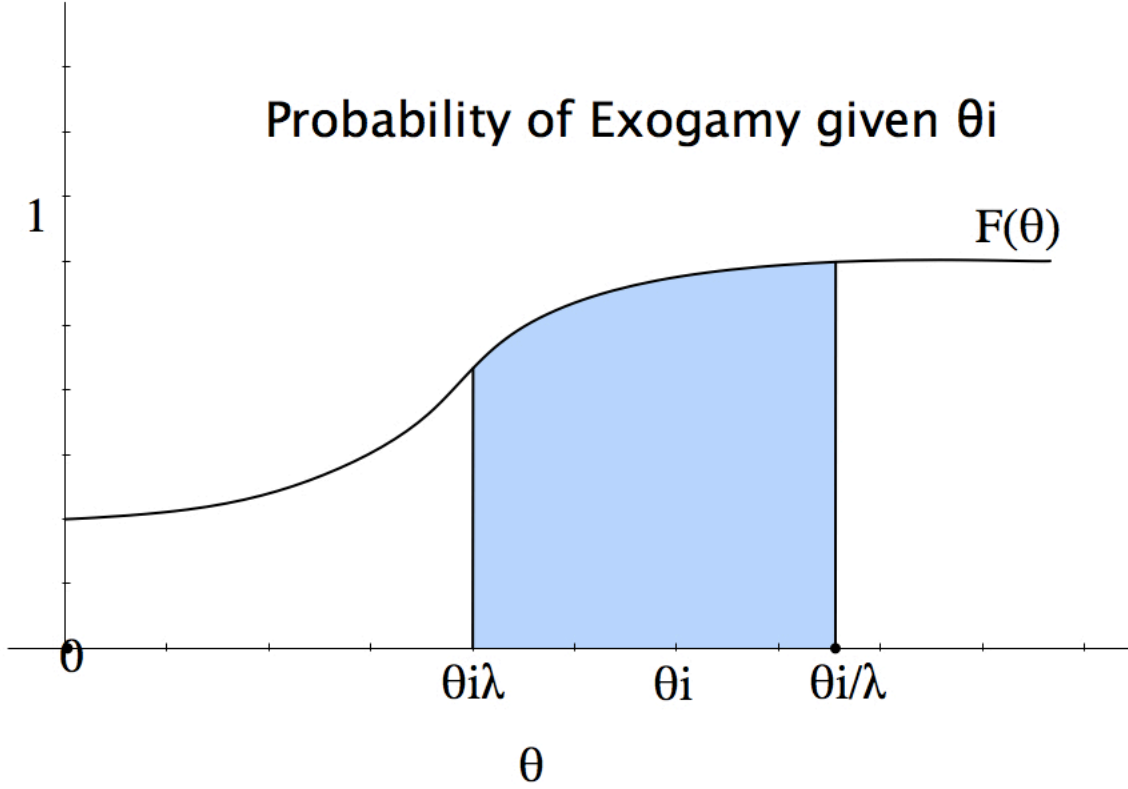
I now assume that all candidates are able to physically display a signal of their quality. The environment is unchanged except that before entering the marriage market, each candidate transmits a signal of publicly observable magnitude,  $l_i \in [0, \infty)$ . The cost of the signal to candidate  $i$  is  $c(l, \theta_i)$ .  $c(\cdot)$  is twice continuously differentiable,  $c_1(l, \theta_i) > 0$   $c_2(l, \theta_i) < 0$ . Assume for now that  $c(\cdot)$  supports a perfectly separating equilibrium.

The payoffs are 5, with signaling costs subtracted:

$$U_i = \left\{ \begin{array}{ll} \theta_j - c(l_t^i, \theta_t^i) & \text{iff } y = (1, 1) \\ (1 - \delta) \theta_i - c(l_t^i, \theta_t^i) & \text{iff } y \neq (1, 1) \end{array} \right\} \quad (9)$$

The period game is as follows:

1. Each candidate observes their own quality,  $\theta_t^i$ .
2. Each candidate chooses  $l_t^i \in \mathcal{L}$ , and pays the associated cost:  $c(l_t^i, \theta_t^i)$
3. Each candidate observes the other's signal,  $l_t^j$
4. Candidates simultaneously choose  $y_t^i, y_t^j$
5. Exogamous marriage occurs iff  $y_t = (1, 1)$



**Lemma 4.** *The ex ante probability of exogamous marriage is equal to:*

$$p(y = (1, 1) | \delta) = \int \left[ F\left(\frac{\theta}{1-\delta}\right) - F((1-\delta)\theta) \right] dF(\theta) \quad (10)$$

*Proof.* A candidate with quality  $\theta_i$  will marry exogamously if and only if  $\theta_j > (1-\delta)\theta_i$ .

It follows directly from 5.1 that  $y = (1, 1)$  if and only if  $\frac{\theta_i}{1-\delta} > \theta_j > (1-\delta)\theta_i$ . It follows trivially that the probability of exogenous marriage, conditional on  $\theta_i$ , is the cumulative distribution function evaluated from  $\frac{\theta_i}{1-\delta}$  to  $(1-\delta)\theta_i$ . That is,  $p(y = (1, 1) | \theta_i, 1-\delta) = F\left(\frac{\theta_i}{1-\delta}\right) - F((1-\delta)\theta_i)$ .

To calculate the unconditional probability of exogamous marriage, just integrate this function over all possible values of  $\theta_i$ :

$$\frac{\partial p(y=(1,1)|\delta)}{\partial(1-\delta)} = \int_0^{\theta_{max}} \left[ -\frac{f\left(\frac{\theta_i}{1-\delta}\right)}{(1-\delta)^2} - (1-\delta)f((1-\delta)\theta_i) \right] dF(\theta_i) < 0 \quad \square$$

**Lemma 5.**  $p(y = (1, 1) | (1-\delta))$  is strictly increasing in  $\delta$ .

*Proof.* available in appendix □

The agent solves two problems, in the following order:

1.

$$\max_{l_i \geq 0} E(y_i [\theta_j - \delta \theta_i] | l_i) - c(l, \theta_i)$$

2.

$$\max_{y_i \in \{0,1\}} E(y_i [\theta_j - (1 - \delta) \theta] | l_j)$$

The first problem is to choose the strength of the signal of quality. The second problem is to choose  $y_i$ . At the time of the market interaction the signaling cost is sunk, so it will not have any effect on the exogamy decision,  $y_i$ . The optimal strategy can be solved for via backward induction, as follows:

At stage 2, the agent has a dominant strategy:  $\sigma(\theta_i, \theta_j, \delta) = 1$  if and only if  $\theta_j > (1 - \delta) \theta_i$ .

At stage 1, the agent solves the following problem:  $\max_{l_i \geq 0} E(y_i [\theta_j - (1 - \delta) \theta_i] | l_i) - c(l, \theta_i)$ .

The cost function is such that the solution to this problem is  $l^*(\theta)$ , with a positive first derivative everywhere.

$$\text{As in sections 4 and 5, } 1 - \delta_{t+1} = \left\{ \begin{array}{ll} 1 & \text{if } y = (1, 1) \text{ and } 1 - \delta_t + \epsilon > 1 \\ 1 - \delta_t + \epsilon & \text{if } y = (1, 1) \text{ and } 1 - \delta_t + \epsilon \leq 1 \\ 1 - \delta_t - \epsilon & \text{if } y \neq (1, 1) \text{ and } 1 - \delta_t - \epsilon > 0 \\ 0 & \text{if } y \neq (1, 1) \text{ and } 1 - \delta_t - \epsilon \leq 0 \end{array} \right\}.$$

**Proposition 5.**

There exists a unique value of  $\delta$  for which  $\dot{\delta}(t) = 0$ . This value,  $\delta_s^*$ , solves

$$\int_0^{\theta_{max}} \left[ F\left(\frac{\theta_i}{(1 - \delta)}\right) - F((1 - \delta) \theta_i) \right] dF(\theta_i) = \frac{1}{2} \quad (11)$$

Furthermore, for all  $\delta > \delta_s^*$ ,  $\dot{\delta}(t) < 0$ , and for all  $\delta < \delta_s^*$ ,  $\dot{\delta}(t) > 0$ . Therefore,  $\delta_t \rightarrow \delta_s^*$ .

Regardless of its initial value, over time  $\delta$  will converge to  $\delta_s^*$ .

*Proof.* available in appendix. □

**Lemma 6.**

$$\dot{\delta}(t) = - \left\{ 2 \left[ \int_0^\infty \left[ F \left( \frac{\theta_i}{1-\delta} \right) - F((1-\delta)\theta_i) \right] dF(\theta_i) \right] - 1 \right\} \quad (12)$$

*Proof.* available in appendix. □

## 6 Comparison and Conclusion

### 6.1 Comparing Equilibrium Inbreeding Levels

I assume now that the quality distribution is uniform on the interval  $[0, \frac{1}{a}]$ .

In this section, I compare the steady state factors of inbreeding depression,  $\delta^*$ ,  $\delta_a^*$ ,  $\delta_s^*$ .

I show that for this quality distribution, the highest (worst) steady state  $\delta$  is for non-adverse to endogamy, non signaling population. The next highest steady state is  $\delta$  is that of the adverse to endogamy, non-signaling population,  $\delta_a^*$ . The lowest steady state is that of the adverse to endogamy, signaling population, with  $\delta_s^*$ .<sup>1</sup>

**Proposition 6.** *For a uniform distribution with min quality of zero and maximum quality  $\frac{1}{a}$ ,  $1 = \delta^* > \delta_a^* > \delta_s^* > 0$ .*

*Proof.* Directly from  $10 = \delta^*$ .

From 8:  $1 - \delta_a^* = \frac{\sqrt{2} \int_0^{F^{-1}(1/\sqrt{2})} x dF(x)}{F^{-1}(1/\sqrt{2})}$ . Assume any uniform distribution of qualities with minimum

0 and maximum  $\frac{1}{a}$ :  $f(x) = \begin{cases} a & \text{for } x \leq \frac{1}{a} \\ 0 & \text{for } x > \frac{1}{a} \end{cases}$ , and  $F(x) = \max \left\{ ax, 1 \right\}$ . Therefore:  $1 - \delta_a^* =$

$\frac{\sqrt{2} \int_0^{\frac{1}{a\sqrt{2}}} x dx}{\frac{1}{a\sqrt{2}}}$  which implies that  $1 - \delta_a^* = \frac{1}{2}$

From 11:  $\int_0^{\theta_{max}} \left[ F \left( \frac{\theta_i}{1-\delta_s^*} \right) - F((1-\delta_s^*)\theta_i) \right] dF(\theta_i) = \frac{1}{2}$ . With a uniform distribution of qualities this implies  $\Rightarrow \frac{1}{2} = \int_0^{\frac{1}{a}} \left[ a \left( \frac{\theta_i}{1-\delta_s^*} - \theta_i(1-\delta_s^*) \right) \right] ad(\theta_i)$  which implies  $1 - \delta_s^* = \frac{\sqrt{5}-1}{2} \simeq 0.62$

Clearly,  $1 > 0.62 > 0.5 > 0$ , and therefore  $1 > \delta_a^* > \delta_s^* > 0$ .

Therefore  $1 = \delta^* > \delta_a^* > \delta_s^* > 0$ . □

---

<sup>1</sup>Human quality would most plausibly be distributed normally, with a left truncation at quality zero. Those with quality less than zero would not be observed because they would be dead. Unfortunately, it is difficult to calculate  $\delta_s^*$  and  $\delta_a^*$  explicitly for a left truncated normal distribution, because it does not integrate easily.

## 6.2 Conclusion

From the transition to hunting until the first transition to agriculture, a period of roughly 1.8 million years, all Homo Sapiens were hunter-gatherers[15]. Evolution by natural selection for fitness in a foraging environment has had a profound influence on all human traits, including anatomical structures, cognitive abilities and preferences. This paper demonstrates how past economic and environmental conditions can shape human traits. Conversely, and with some caution, clues to past economic conditions can be found in modern preferences and physical appearance.

It seems likely that our earliest hunting ancestors had depressed fitness due to inbreeding. Some human preferences and physical traits may have evolved partially as a response to this problem. Both individual and group selection would have favoured a display of moderately costly signals, as well as marriage market preferences for larger signals. These conclusions are qualitatively consistent with observed human traits, as well as preferences over those traits.

## References

- [1] G.A. Akerlof. The market for "lemons": Quality uncertainty and the market mechanism. *The quarterly journal of economics*, pages 488–500, 1970.
- [2] J.S. Banks and J. Sobel. Equilibrium selection in signaling games. *Econometrica: Journal of the Econometric Society*, pages 647–661, 1987.
- [3] N. Barber. The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Ethology and Sociobiology*, 16(5):395–424, 1995.
- [4] C.T. Bergstrom, S. Számadó, M. Lachmann, C.T. Bergstrom, S. Számadó, and M. Lachmann. Separating equilibria in continuous signalling games. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 357(1427):1595–1606, 2002.
- [5] Felix Breden and Michael J Wade. Inbreeding and evolution by kin selection. *Ethology and Sociobiology*, 2(1):3–16, 1981.
- [6] D. Charlesworth and B. Charlesworth. Inbreeding depression and its evolutionary consequences. *Annual review of ecology and systematics*, 18:237–268, 1987.
- [7] I.K. Cho and D.M. Kreps. Signaling games and stable equilibria. *The Quarterly Journal of Economics*, 102(2):179–221, 1987.
- [8] S.T. Emlen, L.W. Oring, et al. Ecology, sexual selection, and the evolution of mating systems. *Science*, 197(4300):215–223, 1977.
- [9] A. Grafen. Biological signals as handicaps. *Journal of theoretical biology*, 144(4):517–546, 1990.
- [10] W.D. Hamilton. Altruism and related phenomena, mainly in social insects. *Annual Review of Ecology and systematics*, 3:193–232, 1972.
- [11] A.L. Hughes. Preferential first-cousin marriage and inclusive fitness. *Ethology and Sociobiology*, 1(4):311–317, 1980.

- [12] A. Johnson and T. Earle. *The evolution of human societies: from foraging group to agrarian state*. Stanford University Press, 2000.
- [13] G.F. Miller. How mate choice shaped human nature: A review of sexual selection and human evolution. *Handbook of evolutionary psychology: Ideas, issues, and applications*, pages 87–129, 1998.
- [14] A.P. Møller, M. Soler, and R. Thornhill. Breast asymmetry, sexual selection, and human reproductive success. *Ethology and Sociobiology*, 16(3):207–219, 1995.
- [15] H. Ofek. *Second nature: economic origins of human evolution*. Cambridge University Press, 2001.
- [16] Michael Peters. The pre-marital investment game. *Journal of Economic Theory*, 137(1):186–213, 2007.
- [17] Anne Pusey and Marisa Wolf. Inbreeding avoidance in animals. *Trends in Ecology & Evolution*, 11(5):201–206, 1996.
- [18] Joseph Shepher. Mate selection among second generation kibbutz adolescents and adults: Incest avoidance and negative imprinting. *Archives of sexual behavior*, 1(4):293–307, 1971.
- [19] M. Spence. Job market signaling. *The quarterly journal of Economics*, 87(3):355–374, 1973.
- [20] L.V. Spencer, J.P. Callen, et al. Hair loss in systemic disease. *Dermatologic clinics*, 5(3):565, 1987.
- [21] A. Zahavi. Mate selection—a selection for a handicap. *Journal of theoretical Biology*, 53(1):205–214, 1975.