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Gianni De Fraja, University of Leicester and CEPR

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Centre for Economic Policy Research
90–98 Goswell Rd, London EC1V 7RR, UK
Tel: (44 20) 7878 2900, Fax: (44 20) 7878 2999
Email: cepr@cepr.org, Website: www.cepr.org

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ABSTRACT

The Origin of Utility*

This paper proposes an explanation for the universal human desire for increasing consumption. It holds that it was moulded in evolutionary times by a mechanism known to biologists as sexual selection, whereby a certain trait – observable consumption – is used by members of one sex to signal their unobservable characteristics valuable to members of the opposite sex. It then goes on to show that the standard economics problem of utility maximisation is formally equivalent to the standard biology problem of the maximisation of individual fitness, the ability to pass genes to future generations.

JEL Classification: D63 and I28

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Gianni De Fraja
Department of Economics
University of Leicester
Leicester
LE1 7RH
Tel: (44 116) 252 3909
Fax: (44 116) 252 2908
Email: defraja@le.ac.uk

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1 Introduction

Individuals strive to maximise an increasing function of consumption. Standard as it is in economics, this assumption however perplexes other scientists: “Western economics usually assumes that individuals are out to maximise personal gains, but where is the scientific justification for this assumption? And what exactly is ‘personal gain’?” (Trivers 1985, p 1). Trivers’ doubts are spelt out more explicitly by Grafen (1998, p 441): “The formulation of the dynastic utility function in terms of consumption purely for its own sake is inconsistent with the biological viewpoint”. The inconsistency is the apparent lack of any survival or reproductive advantage, which, like any physical or behavioural trait, maximisation of consumption for its own sake would have to afford in order to develop and persist.

In this paper I propose a foundation for the human desire of consumption rigorously based on evolutionary arguments, and therefore consistent with the biological viewpoint. This approach follows an established economics tradition which studies human behaviour through evolutionary lenses by looking for fitness advantages in the conditions facing early humans.¹ The universality of the desire for consumption across cultures and continents and the view of evolutionary psychology regarding the speed of adaptations (Barrett et al 2002 p 12) indicate that this trait must indeed have developed well before the dispersion of early humans from Africa, around 80,000 years ago. Unlike the papers cited in the footnote, I suggest here that there are reproductive, not survival, benefits of the trait studied. Specifically, I argue that the desire for consumption for its own sake is driven by sexual selection by mate choice. This is an evolutionary mechanism by which different individuals of one sex enjoy different reproductive success as a consequence of the mating choice of the individuals

¹Alchian (1950, pp 213-214) and Friedman (1953) viewed profit maximisation as a selection mechanism for firms. More recently, evolutionary advantages have been suggested for many human traits. Examples include altruism (Becker 1976, Frank 1987, Bergstrom 1995, Bester and Guth 1998, Eswaran and Kotwal 2004), risk-taking (Robson 1995, Dekel and Scotchmer 1999, Warneryd 2002), experimentation (Robson 2001b), individualistic (as opposed to interdependent) preferences (Ok and Vega-Redondo 2001), the rate of intertemporal preferences (Hansson and Stuart 1990, Rogers 1994, Trostel and Taylor 2001), the dependence of utility on the presence of salient unchosen alternatives (Samuelson and Swinkles 1996) intergenerational cultural transmission (Bisin and Verdier 2001) and resource flows (Robson and Kaplan 2003), and more generally, the structure and development of the family (Bergstrom 1996), the emergence of trade (Ofek 2001, Seabright 2004, Horan et al 2005), economic growth (Galor and Moav 2002).

of the opposite sex. This mechanism is the driving force for the development of traits which are differentiated by sex and have zero or negative survival value:² from the extravagant tail feathers of pheasants, paradise birds, peacocks and many other birds, to the ritual dancing and hopping displays in “leks”, to the courtship vocalisations in tigers, deer, crickets, frogs, to the flashing of fireflies, to the complex bowers built and decorated by bowerbirds; to human traits such as the male beard and the female breasts.³

Zahavi (1975) provided a solid game theoretic foundation for sexual selection. He realised that advertisement by males must be costly, exactly in the sense in which a signal is costly in the economics literature (Spence 1973): the higher an individual’s quality, the less burdensome it is for him to incur the cost of the signal, and the stronger the signal he will issue to distinguish himself from his lesser rivals in the eye of the females. Zahavi argued that the reproductive benefit accruing to a male who is more likely to be chosen by females may well outweigh the cost incurred by issuing the signal.

Consumption for its own sake, I argue here, is precisely such a signal. It is easy to observe and expensive to acquire, and has served, throughout history, as an indicator of an individual’s desirability as a mate. Veblen (1899) identified

² “It is to the female’s advantage to be able to pick the most fit male available for fathering her brood. Unusually fit fathers tend to have unusually fit offspring. One of the functions of courtship would be the advertisement, by a male, of how fit he is. A male whose general health and nutrition enables him to indulge in full development of secondary [not physiologically necessary for reproduction] sexual characters [...] is likely to be reasonably fit genetically [...] In submitting only to a male with such signs of fitness a female would probably be aiding the survival of her own genes” (Williams 1966, p 184).

³ See Zahavi and Zahavi (1997) for many more examples, or Andersson (1994, p 10 and Table 6.A, pp 132-142), for a taxonomy of the various mechanisms, from mate choice to male contests. Darwin devoted much of the *Descent of Man* (1871) to it, but, unlike natural selection, sexual selection was rejected for a long time by the scientific community (Anderson 1994, pp 17-19), possibly because Darwin did not offer a persuasive explanation of the mechanism through which sexual selection operates, simply appealing to the aesthetic sense of the females of the species (1871, last chapter). Fisher (1930) reprised Darwin’s idea, and did describe a plausible mechanism through which it might operate. Called the “runaway process” or the “sexy son hypothesis”, it is in the spirit of the herd theory: if all females prefer certain males, then it pays a female with no preference also to choose those males as mates, because her sons will need to attract the current females’ daughters, who will inherit their mother’s preferences, and will be more likely to do so if they inherit their father’s genes. This idea is not fully satisfactory either: it cannot explain which direction the process takes, and in the absence of a cost of acquiring the trait, all males will tend to possess the optimum level as generations go by: the observation of variation across individuals would need to be justified by evolution not having yet completed its course.

clearly the importance of expensiveness and wastefulness of consumption: inexpensive items are not, *cannot* be effective signals, precisely because their very inexpensiveness makes it possible for everyone to sport them.⁴ Unlike Veblen, recent economic analysis has had access to Fisher’s and Zahavi’s insights, and yet has neglected the role of sexual selection as a powerful engine of human evolution.⁵

Building on Veblen’s analysis, Bagwell and Bernheim (1996) and Corneo and Jeanne (1997), among others, have posited that conspicuous consumption of goods such as luxury goods, which are “completely novel in evolutionary terms”, enhances status, and that status is evolutionary “hard-wired” to affect *directly* an individual’s utility (Robson 2001a p 24). Postlewaite (1998)⁶ prefers, on the grounds of parsimony, an approach with the opposite casual direction: desire for consumption is hard-wired, and status “is instrumental in determining ultimate consumption levels” (p 785, the marriage model in Cole *et al.* 1992 is built on this view). My paper complements these views by answering the question: how *did* concern with consumption, or with status, become hard-wired? Fearing snakes, throwing projectiles accurately, liking sweet foods all became hard-wired because individuals carrying the genes that determine these behaviours were more likely to pass these genes to future generations. The biologist’s distinction between proximate and ultimate cause is useful here: the *proximate* cause of us liking sugar is the network of messages from the taste buds to the brain stimulated by the chemical composition of some components of sugar which creates a pleasurable reaction, well understood by biochemists.

⁴His books are rich in examples. “The chief use of servants is the evidence they afford to the master’s ability to pay”, rather than helping him in any useful manner (Veblen 1899, p 62). Their cumbersome liveries and unwieldy uniforms are actually designed to prevent them from performing any useful or productive activity. Similarly, skirts persist tenaciously as fashion accessories because, not despite, they “hamper the wearer at every turn and incapacitate her for all useful exertion”, thus unmistakably demonstrating that she does not need to work (p 171). Corsets and top hats are among his other examples. By the same token, in many animal species, powerful males obtain and protect large territories, much larger than it can be possibly be necessary to provide food and shelter to the family and subordinate individuals (O’Donald 1963, Zahavi and Zahavi 1997, pp 28-29). This is of course a very accurate description of the behaviour of human ruling classes nowadays and over the entire course of history.

⁵For example, in his seminal economic analysis of human evolution, Frank notes how sexual selection traps a species into a prisoner’s dilemma (“peacocks *taken as a group* would clearly do better if all had smaller tail feathers” p 23), but otherwise does not link it to human evolution, as other social scientists have done (Miller 2000, Ridley 2003, Buss 2004).

⁶This paper hints at some of the ideas presented here, see pp 781–782.

But the *ultimate* cause is the fact that, over countless generations, individuals who liked sugar had a survival advantage, well understood by biologists, over those who did not. In this perspective we can also easily understand why we love our own children, even in the absence of any personal survival advantage of this trait: genes that make an individual love his children are more likely to populate future generations. But why consumption for its own sake? Where is the evolutionary benefit of coveting goods? The *proximate* cause of our desire to consume is of course the pleasurable sensation deriving from the possession and display of beautiful, comfortable, rare, precious and luxurious goods. I argue here that the *ultimate* cause is sexual selection: individuals who had a stronger desire for consumption for its own sake were more likely to be chosen as mates by members of the opposite sex, and hence more likely to pass on to future generations the genes inducing them to desire goods.

In section 2, I present a mathematical model, inspired by Grafen (1990), which captures these ideas. It describes a population composed of males and females, where the males' reproductive potential is limited by female choice. Males differ in their value to females, and face a trade-off between wasteful "conspicuous" consumption and unobservable activities which enhance their chance of survival. Females observe males' conspicuous consumption, and choose with whom to mate. In a "signalling equilibrium" (Section 3), males undertake conspicuous consumption in order to signal their quality to females, and females are more likely to mate with males whose observed consumption is higher. Proposition 4 in Section 4 identifies the conditions which the population must satisfy in order for a signalling equilibrium to exist. While not readily interpretable, they can well be violated, implying that only some combinations of genotypes and environmental constraints can give rise to the development of consumption as a Zahavian handicap.

The formal analysis is completed in Section 5, where I show a natural connection between maximisation of fitness and maximisation of a utility function with consumption bundles as arguments. More precisely, I show that the trade-off between survival and reproduction can be mapped one-to-one with the trade-off between "survival consumption" and "conspicuous consumption". This provides an evolutionary foundation to the indifference maps that constitute the basis of the economic analysis of consumer behaviour, and suggests that preferences are not arbitrary, but have evolved in response to our ancestors' exogenous constraints. Section 6 discusses some empirical evidence and considers some open economics questions in the light of the ideas of the paper.

2 The Model

2.1 The population

As Grafen in his seminal paper (1990), I consider a sexually reproducing population, comprising two sexes, males and females. They meet and mate in a “mating season”, divided into $T > 1$ discrete periods. The interpretation of season and periods within a season is flexible: the season could be the summer and the periods days; alternatively, the season could be a generation, and each period an oestrus cycle. Offspring are born and reared after the end of the mating season. Within the season, the population dynamics from period to period is governed by survival and mating. In each period, matching is one-to-one: each individual is matched to at most one individual of the other sex. Matching probabilities in period t depend on the population numbers of the two sexes, given by F_t for females and M_t for males. Specifically, a female is matched to a male with probability $q_F(F_t, M_t)$, and a male is matched to a female with probability $q_M(F_t, M_t)$. A matched pair will mate if the benefit exceeds the cost for both parties. In humans, like in many other sexual species, the opportunity cost of mating differs in the two sexes,⁷ and consequently so does parental investment. I capture this asymmetry with the extreme assumption of a polyginous species with no paternal investment. Thus a male has no opportunity cost of mating, and agrees to mate every time he is matched with a female, returning to the mating market in the following period. This is not so for a female: to reproduce successfully, maternal investment is necessary, in the form of pregnancy, lactation and other childcare activities; I assume that each female can have at most one reproductive cycle per season, and that they leave the “market” if they mate. In Dixit and Pyndick’s terminology (1994), mating in a period (except the last) kills the option of mating with a male of superior quality later in the season. In addition, both males and females may die during the season.

Individuals of both sexes differ in their idiosyncratic characteristics, which affect their fitness, loosely defined as the individual’s ability to propagate their genes, and their chances of survival from one period to the next.

⁷This difference is itself a consequence of anisogamy, the fact the sexual cells (gametes) have asymmetric sizes in the two sexes: this in turn can be explained as a consequence of the dynamic instability of an equilibrium where gametes have the same size (Maynard Smith 1978), and is a widely open area of research in evolutionary biology (Czárán and Hoekstra 2004).

- Males differ in a quality, measured by a single dimensional parameter, θ , which, at the beginning of period t in the season, is distributed in $[\theta_{\min}, \theta_{\max}] \subseteq \mathbb{R}$, according to the density $\phi_t^M(\theta) > 0$ for $\theta \in [\theta_{\min}, \theta_{\max}]$, and distribution $\Phi_t^M(\theta)$, with $\phi_t^M(\theta) = \frac{d\Phi_t^M(\theta)}{d\theta}$, which satisfies $\frac{d}{d\theta} \left(\frac{k - \Phi_1^M(\theta)}{\phi_1^M(\theta)} \right) < 0$, for every $k \in [0, 1]$, a slightly stronger version of the assumption of a monotonic hazard rate. The total number of males in period t , $t = 1, \dots, T$, is denoted by M_t .
- Females differ in their potential for survival and maintain fertility during the season. Specifically, let δ be a fertile female's probability of surviving and remaining fertile for one further period of time.⁸ In period t , δ is distributed in $[0, 1]$, according to density $\phi_t^F(\delta)$ and distribution $\Phi_t^F(\delta)$, with $\phi_t^F(\delta) = \frac{d\Phi_t^F(\delta)}{d\delta}$. F_t is the total number of females in period t , $t = 1, \dots, T$.

At the beginning of the season, the number and characteristics of the adults of both sexes is fixed. Thus $\phi_1^M(\theta)$ ($\phi_1^F(\delta)$) is the density of males (females) of quality θ (of survival rate δ) who survive from birth to the beginning of the next season.

The benefit of mating is measured by a function $v(\theta)$, satisfying $v'(\theta) > 0$, a normalisation, and $v(\theta_{\min}) > 0$, mating is always better than not mating. There is no gain in generality in having differential benefits for males and females. As shown by Grafen (1990, pp 489-491), maximisation of the expectation of $v(\theta)$ is the evolutionary stable strategy equilibrium.⁹

Following Grafen (1990), I assume that the dynamics of survival from one season to the next and of new births, taking interrupted gestations and early deaths into account, determine the same distribution of types as at the beginning of the previous season, both for females and for males.¹⁰ Sufficient, but

⁸There is little gain in generality if the survival rate may vary from one period to the next.

⁹This is the central game theory concept in biology. An evolutionary stable strategy (ESS) is such that, if all members of a population adopt it, no mutant strategy can obtain a higher payoff. In an ESS equilibrium, all players adopt the ESS, and the population cannot be invaded by any competing alternative strategy. This is a refinement of the concept of Nash equilibrium: each individual maximises fitness under the existing constraints (Maynard-Smith and Price 1973).

¹⁰Grafen introduces this assumption in order to obtain an equilibrium based on the handicap principle, operating independently of the Fisher runaway process, mentioned in footnote 3: if the probability density function of the offspring types is independent of the parents' types, then, by construction, the Fisher effect cannot operate.

not necessary, to ensure this is the absence of all adults from the new mating season, and lack of correlation between the fathers' and the sons' θ 's. The latter does not of course imply that the father's type is unimportant: think of θ as reducing the likelihood of birth defects or early age diseases in offspring, and of $v(\theta)$ as the expected *number* of offspring who survive to adulthood and enter the market at the beginning of the next season, which therefore increases with θ . Each offspring's type is then drawn from a distribution invariant to the father's type, determined, for example, by the environment. This mechanism does not imply absence of natural selection either: what is passed on to the next generation is not the genes that determine θ , but rather the genes that determine the link between θ and the strategy followed by males.

2.2 Males' optimal strategy.

Males choose¹¹ two variables, conspicuous consumption $c \in \mathbb{R}_+$, and investment in survival activities, measured by a variable $w \in \mathbb{R}_+$, for example the consumption of high energy food, the search and adaptation of suitable shelter, or the accumulation of hidden reserves of food. w increases the chances of survival: in each period, a male survives with probability $\pi(w) \in (0, 1)$, with $\pi'(w) > 0$ and $\pi''(w) \leq 0$. Conspicuous consumption is wasteful: it has no direct benefit, but has a cost, described by a standard production possibility frontier: for every $(c, w, \theta) \in \mathbb{R}_+^2 \times [\theta_{\min}, \theta_{\max}]$:

$$f(c, w, \theta) = 0, \tag{1}$$

with $f_c(\cdot), f_w(\cdot) > 0$, to capture the trade-off between c and w , and $f_\theta(\cdot) < 0$, to indicate that higher qualities are associated with expanded production possibility frontiers. Females can observe c only: they can see a male's consumption, but cannot gauge exactly how much body fat a male has, or the quality of his shelter, nor can they determine directly his quality θ . The role of c is therefore to serve as a signal. The formal game-theoretic representation of a strategy in a signalling game as a mapping from the set of possible types to the set of

¹¹The term "choose" is typically used in signalling models in economics, but it is also appropriate in the current more biological set-up, where it does not have the implication of conscious decision making which human choice has. Thus the peacock is said to choose the length of his tail, the deer the size of his antlers, the frog the depth of his call, the fish the intensity of his coloration, even though these choices are best described as manifestations of the phenotype, and determined by the interaction of the genotype (the DNA instructions) with the environment.

admissible actions matches closely the biological definition of allele as a set of instructions specifying the response of the individual hosting that allele to the environment.¹² Formally, males' strategy set is the set of all mappings from the space of types $[\theta_{\min}, \theta_{\max}]$ to the space of possible signals, or equivalently, the set of all possible alleles that specify the behaviour to be followed by genotype θ . Males' strategies are denoted by $c(\theta)$. In a signalling equilibrium, described formally in the next section, females infer correctly the males' types from their observed signal, c , and males choose the best signal, correctly basing their calculation on the females' beliefs about their type.¹³

From (1) it is convenient to define the function $\omega : \mathbb{R}_+ \times [\theta_{\min}, \theta_{\max}] \rightarrow \mathbb{R}_+$, which associates to a signal c and a type θ the (maximum) level of w that individual of type θ who emits signal c can acquire: $\omega(c, \theta)$ is the solution in w of (1).

The males' action set does not contain the display of observable survival resources. This display occurs frequently in humans and other species (Yosef 1991), and could be included in the model by an additional argument in the production possibility frontier (1), say r , thus writing $f(c, w, \theta, r)$. While not altering the qualitative characteristics of the equilibrium, doing so would add considerable complication: with this additional choice, c and θ would not be sufficient to determine the remaining variables, w and r , in the way the function ω uniquely determines w . The fundamental, plausible, feature of the model is the presence of *some* unobservable aspect of males' phenotype, measured here by w . Without it, for example if w were the same for all males, the species would be in a trivial equilibrium where males choose $c = 0$, and females observe r and infer correctly a male's θ from inverting $f(0, w, \theta, r)$.

2.3 Females' optimal strategy.

In each period, a female matched to a male has a very simple action set: either she mates or she does not mate. Her choice depends on her survival probability δ and her belief about the type of the male she is matched with. Beliefs in period t can be described by the function $c_t^b(\theta)$, the signal expected from a

¹²The environment includes also the individual's characteristics: the same allele specifies the individual's behaviour according to the individual's sex and characteristics.

¹³As in Grafen (1990), the game described so far has a non-signalling equilibrium where $c(\theta) = 0$ for every $\theta \in [\theta_{\min}, \theta_{\max}]$, and where females' out of equilibrium beliefs are sufficiently pessimistic: for example, females associate type θ_{\min} with any signal $c > 0$. In what follows I concentrate on the signalling equilibrium.

male of type θ .¹⁴ Formally, let $V_t^F(\delta)$ be the expected payoff of a female for participating in the mating market in the next period, that is from period $t + 1$.

Definition 1 For given beliefs $c_t^b(\theta)$, define the acceptance function, $\alpha_t(\delta)$, as the higher of θ_{\min} and of the solution in θ to:

$$v(\theta) = \delta V_t^F(\delta). \quad (2)$$

The acceptance function summarises the strategy followed by females, and can be drawn in Figure 1 using Lemma 1.

Lemma 1 For every $t < T$: there exists $\underline{\delta}_t > 0$, such that $v(\theta_{\min}) = \underline{\delta}_t V_t^F(\underline{\delta}_t)$; there exists $\bar{\theta}_t \in [0, 1]$, such that $\bar{\theta}_t = v^{-1}(V_t^F(1))$; the function $\alpha_t(\delta)$ is strictly increasing in $[\underline{\delta}_t, 1]$.

Proof. Total differentiation of (2) yields $\frac{d\alpha_t(\delta)}{d\delta} = \frac{V_t^F(\delta) + \delta V_t^{F'}(\delta)}{v'(\theta)} > 0$ whenever $\alpha_t(\delta) > \theta_{\min}$, thus establishing the last assertion in the Lemma. It also shows that there can be at most one value $\delta \in [0, 1]$ such that (2) holds, and $v(\theta_{\min}) > 0$ implies the first assertion. Since v is the same in each period, the maximum future payoff cannot exceed $v(\theta_{\max})$, implying the second assertion and establishing the Lemma. ■

Because $v(\theta)$ is strictly increasing, a female of type δ , matched with a male of type θ , mates with him if $\theta > \alpha_t(\delta)$, and does not mate if $\theta < \alpha_t(\delta)$. In words, a female agrees to mate with a male believed to be of type θ , if her payoff for mating, $v(\theta)$, as at least as big as the payoff for not mating.¹⁵ Lemma 1 can be used to represent females' strategy in the (δ, θ) -cartesian plane: all females of type $\delta < \underline{\delta}_t$ mate in the current period with any male type θ , and all females matched with a sufficiently "good" male mate with him (note that, in general, $\bar{\theta}_t$ is strictly below θ_{\max}). This is summarised in Figure 1: male-female matches such that the combination of types (δ, θ) is in the light grey area mate, those in the dark area do not.

¹⁴Given a priori regarding males' types $\phi_t^M(\theta)$, and given a belief about the signal $c_t^b(\theta)$ issued by male of type θ , the posterior density function $c = c_t^b(\theta)$, is given by $\frac{\phi_t^M(\theta^k)}{\sum_{h=1}^H \phi_t^M(\theta^h)}$, if $c_t^{b-1}(c)$ has measure 0 and the image set of $c_t^{b-1}(c)$ is $\{\theta^1, \dots, \theta^h, \dots, \theta^H\}$, and 0 otherwise. If instead $c_t^{b-1}(c)$ has positive measure, then the density of the posterior is given by: $\frac{\phi_t^M(\theta)}{\int_{\theta_{\min}}^{\theta_{\max}} \phi_t^M(\theta) d\theta}$.

¹⁵If $\theta = \alpha_t(\delta)$ she is indifferent. This is a measure 0 case, and, for definiteness, I assume that she mates with probability 1 in this case.

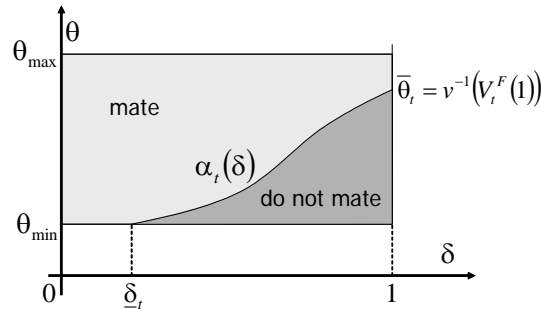


Figure 1: Female choice in period t .

The model differs from Grafen's (1990) where females are all identical, and where males' strategy is independent of the time in the mating season.¹⁶ His model and mine share the fundamental asymmetry between forward looking females –whose maximisation strategy involves the exercises of an option, and therefore the forecast of future conditions–, and here-and-now males –for whom the opportunity cost of mating in the present period is lower.

3 Signalling Equilibrium.

After defining the equilibrium in general terms, the next section derives it for a simplified set-up with two periods only in the mating season.

The dynamic behaviour within a season is fully described by a sequence of array of functions, the actions, beliefs and distributions in each period, and a sequence of pairs, the population size for male and females.

Definition 2 Let $\{c_t(\theta), \alpha_t(\delta), c_t^b(\theta), \phi_{t+1}^M(\theta), \phi_{t+1}^F(\theta), V_t^F(\delta)\}_{t=1}^{T-1}$ be a sextuple where $\{c_t(\theta)\}_{t=1}^{T-1}$ is a sequence of signalling functions, $\{\alpha_t(\delta)\}_{t=1}^{T-1}$ is a sequence of acceptance functions, $\{c_t^b(\theta)\}_{t=1}^{T-1}$ is a sequence of female beliefs functions, $\{\phi_{t+1}^M(\theta)\}_{t=1}^{T-1}$ a sequence of density functions with support in $[\theta_{\min}, \theta_{\max}]$, $\{\phi_{t+1}^F(\theta)\}_{t=1}^{T-1}$ a sequence of density functions with support in a subset of $[0, 1]$, and $\{V_t^F(\delta)\}_{t=1}^{T-1}$ a sequence of future payoff functions for females. Let $\{F_t, M_t\}_{t=2}^T$ be a sequence of pairs, denoting the number of females and males participating in the matching in period t .

¹⁶Grafen's model is therefore more directly applicable to traits which cannot be changed readily, such as the plumage or the depth of a frog's call, mine to activities such as dancing, fighting, singing and so on. Certain traits fall in between: a stag's antlers respond slowly to external conditions.

Definition 3 *If the sextuple $\{c_t(\theta), \alpha_t(\delta), c_t^b(\theta), \phi_{t+1}^M(\theta), \phi_{t+1}^F(\delta), V_t^F(\delta)\}_{t=1}^{T-1}$ and the pair $\{F_t, M_t\}_{t=2}^{T-1}$ constitute a signalling equilibrium then, in every period $t = 1, \dots, T-1$, the following conditions¹⁷ hold.*

1. *Every male type θ maximises his expected payoff for the rest of the season by choosing $c_t(\theta)$, in preference to any other available signal.*
2. *For every $\delta \geq \underline{\delta}_t$, $v(\alpha_t(\delta)) = \delta V_t^F(\delta)$.*
3. *For every θ : $c_t(\theta) = c_t^b(\theta)$.*
4.
$$V_t^F(\delta) = q_F(F_{t+1}, M_{t+1}) \int_{\alpha_{t+1}(\delta)}^{\theta_{\max}} v(\theta) \phi_{t+1}^M(\theta) d\theta + [1 - (1 - q_F(F_{t+1}, M_{t+1})) \Phi_{t+1}^M(\alpha_{t+1}(\delta))] \delta V_{t+1}^F(\delta).$$
5.
$$\phi_{t+1}^F(\delta) = \frac{F_t}{F_{t+1}} \delta \phi_t^F(\delta) [1 - q_F(F_t, M_t) [1 - \Phi_t^M(\max\{\alpha_t(\delta), \theta_{\min}\})]],$$
 for every δ .
6.
$$F_{t+1} = F_t \int_0^1 \delta \phi_t^F(\delta) [1 - q_F(F_t, M_t) [1 - \Phi_t^M(\max\{\alpha_t(\delta), \theta_{\min}\})]] d\delta.$$
7.
$$\phi_{t+1}^M(\theta) = \frac{M_t}{M_{t+1}} \pi(\omega(c_t(\theta), \theta)) \phi_t^M(\theta),$$
 for every θ .
8.
$$M_{t+1} = M_t \int_{\theta_{\min}}^{\theta_{\max}} \pi(\omega(c_t(\theta), \theta)) \phi_t^M(\theta) d\theta.$$

In addition: $V_T^F(\delta) = 0$, $\alpha_T(\delta) = \theta_{\min}$, $c_T(\theta) = 0$, $c_T^b(\theta) = 0$.

Condition 1 ensures the allele is not invisable: no alternative allele can obtain a higher payoff, and therefore become prevalent in the population as generations go by. Condition 2 determines the acceptance function in each period, and Condition 3 ensures that along the equilibrium path, females' beliefs are consistent with males' strategies.

The other conditions describe the population dynamic in the course of the mating season. Condition 4 determines recursively the value of a female's option to refrain from mating and remain fertile. To see how it is derived, note that, with probability $q_F(F_t, M_t)$ she will be matched to a male in period t , and with probability $\phi_t^M(\theta)$ this male is of type θ . If $\theta \geq \alpha_t(\delta)$, she will mate with him, and have payoff $v(\theta)$, otherwise she'll postpone again, which happens with probability $\Phi_t^M(\alpha_t(\delta))$, and obtain, in the next period, payoff $V_{t+1}^F(\delta)$. With

¹⁷In order for these conditions to characterise fully the signalling equilibrium, they must be complemented with a specification of the females' out-of-equilibrium beliefs (for example, what they infer if they observe in period t a signal not in the image of c_t). These more technical points are not spelled out in detail.

probability $[1 - q_F(F_t, M_t)]$ she is not matched, in which case her payoff is simply $\delta V_t^F(\delta)$. Putting all of this together the expression in 4 is obtained.

To see how the distribution of females in the next period given in condition 5 is derived, consider females of type δ . At the beginning of period t there are $F_t \phi_t^F(\delta)$ of them. Of these $\delta [1 - q_F(F_t, M_t)]$ are not matched and survive to the next period. Of the $F_t \phi_t^F(\delta) q_F(F_t, M_t)$ who are matched $[1 - \Phi_t^M(\max\{\alpha_t(\delta), \theta_{\min}\})]$ mate and leave the market; of the rest, δ survive and $(1 - \delta)$ die. This applies to every δ , which gives condition 5. The number of females in the market in the next period, F_{t+1} , is given in 6 by straightforward integration of the terms in 5.

Similarly, but more simply, for males: they leave the market only when they die, which happens with probability $\pi(\omega(c_t(\theta), \theta))$. Starting with $M_t \phi_t^M(\theta)$ males of type θ , 7 and 8 are obtained.

According to the last line in the definition, there is no value for females in postponing in the last period, $(V_T^F(\delta) = 0)$, and consequently they all mate with any male they are matched with $(\alpha_T(\delta) = \theta_{\min})$, and so there is no point in males advertising: $c_T(\theta) = 0$, and, for consistency, $c_T^b(\theta) = 0$.

4 Solution in the two period case.

The equilibrium is found by solving simultaneously the large number of equations and differential equations given in the above section. The task remains reasonably tractable when there are only two periods in the mating seasons, whilst maintaining the fundamental asymmetry in the opportunity cost between sexes, and therefore the main conceptual insight for the more general case. Let therefore $T = 2$; with little further loss of generality, also let $F_t = M_t = 1$, there is initially the same number of males and females and $q_F(F_1, M_1) = q_M(F_1, M_1) = 1$: everyone is matched in the first period. To derive the equilibrium in this simpler set-up, we need to determine simultaneously the males' optimal strategy, $c_1(\theta)$, the number of females, F_2 , and males, M_2 , who are seeking a partner in period 2, the value, for a matched female, of postponing mating to period 2, V_1^F , and the density of the distribution of males in period 2. The variables other than $c_1(\theta)$ are immediate from Definition 3:

$$\phi_2^M(\theta) = \frac{1}{M_2} \pi(\omega(c_1(\theta), \theta)) \phi_1^M(\theta), \quad (3)$$

$$M_2 = \int_{\theta_{\min}}^{\theta_{\max}} \pi(\omega(c_1(\theta), \theta)) \phi_1^M(\theta) d\theta, \quad (4)$$

$$\phi_2^F(\delta) = \frac{1}{F_2} \delta \Phi_t^M(\max\{\alpha_1(\delta), \theta_{\min}\}) \phi_1^F(\delta), \quad (5)$$

$$F_2 = \int_0^1 \delta \Phi_1^M(\max\{\alpha_1(\delta), \theta_{\min}\}) \phi_1^F(\delta) d\delta, \quad (6)$$

$$V_1^F = \frac{q_F(F_2, M_2)}{M_2} \int_{\theta_{\min}}^{\theta_{\max}} v(\theta) \pi(\omega(c_1(\theta), \theta)) \phi_1^M(\theta) d\theta. \quad (7)$$

$\underline{\delta}_1$, the type of the least impatient female who mates with any available male, is given by $\underline{\delta}_1 = \frac{v(\theta_{\min})}{V_1^F}$. $\bar{\theta}_1$, the lowest male type such that every female mates with him, is the solution in θ to $v(\theta) = \delta V_1^F$ for $\delta = 1$: $\bar{\theta}_1 = v^{-1}(V_1^F)$.

To determine the males' optimal strategy I use the revelation principle, according to which the optimal strategy is the function $c_1(\theta)$ that maximises a given male's payoff when all other males themselves behave according to $c_1(\theta)$, and when all females believe this to be the case, subject to the incentive compatibility constraint: no male of any type θ would prefer to choose a signal different from $c_1(\theta)$. Intuitively, firstly, if this is the case, then no male has an incentive to deviate, and the females' beliefs are consistent. Secondly, if a candidate equilibrium function $c_0(\theta)$ did not maximise males' payoff, then a population composed of individuals with allele $c_0(\theta)$ would be invisable by an alternative allele. The requirement that no male benefits from choosing a different value of the signal, that is that the requirement that the signal is honest, follows from the revelation principle, which ensures that the search for the payoff maximising male strategy $c_1(\theta)$ can be restricted to functions that reveal each type.

Given the females' optimal strategy, and given that females correctly infer a male's type from the observation of the signal $c_1(\theta)$, consider the options open to a male matched with a female. If he has type $\bar{\theta}_1$ or above, he will mate with probability 1. If he has type $\theta \in [\theta_{\min}, \bar{\theta}_1]$, he mates if and only if the female has type $\delta = \alpha_1^{-1}(\theta)$ or less (see Figure 1), and so he mates with probability $\Phi_1^F(\alpha_1^{-1}(\theta))$. From Definition 3.2, $\alpha_1^{-1}(\theta) = \frac{v(\theta)}{V_1^F}$. This gives the probability of mating for a male of type θ matched to a female as:

$$\begin{cases} \Phi_1^F\left(\frac{v(\theta)}{V_1^F}\right) & \text{for } \theta \in [\theta_{\min}, \bar{\theta}_1) \\ 1 & \text{for } \theta \in [\bar{\theta}_1, \theta_{\max}] \end{cases}.$$

The (season) payoff to a male of type θ is therefore:

$$U(\theta) = \begin{cases} v(\theta) \Phi_1^F\left(\frac{v(\theta)}{V_1^F}\right) + q_M(F_2, M_2) v(\theta) \pi(\omega(c_1(\theta), \theta)) & \text{for } \theta \in [\theta_{\min}, \bar{\theta}_1) \\ v(\theta) + q_M(F_2, M_2) v(\theta) \pi(\omega(c_1(\theta), \theta)) & \text{for } \theta \in [\bar{\theta}_1, \theta_{\max}] \end{cases}. \quad (8)$$

I next determine the condition that ensures that a male will want to signal honestly.

Lemma 2 For $\theta \in [\theta_{\min}, \bar{\theta}_1]$, a male's incentive compatibility constraint is given by:

$$\begin{aligned} \dot{U}(\theta) = & v'(\theta) \Phi_1^F \left(\frac{v(\theta)}{V_1^F} \right) \\ & + q_M(F_2, M_2) [v(\theta) \pi'(\omega(c_1(\theta), \theta)) \omega_\theta(c_1(\theta), \theta) + v'(\theta) \pi(\omega(c_1(\theta), \theta))], \end{aligned} \quad (9)$$

and

$$\frac{dc_1(\theta)}{d\theta} > 0. \quad (10)$$

For $\theta \in [\bar{\theta}_1, \theta_{\max}]$, $c_1(\theta)$ is constant and equal to $c_1(\bar{\theta}_1)$.

Proof. The proof is standard. Suppose a male has true type θ but behaves as if he had type $\hat{\theta}$: to do so, he needs to emit signal $c_1(\hat{\theta})$: this will induce a female to mate with him with probability $\Phi_1^F \left(\frac{v(\hat{\theta})}{V_1^F} \right)$ if $\hat{\theta} < \bar{\theta}_1$, and probability 1 if $\hat{\theta} \geq \bar{\theta}_1$; but it will also change his probability of survival to $\pi(\omega(c_1(\hat{\theta}), \theta))$. His (season) payoff for pretending to be of type $\hat{\theta}$ would therefore be:

$$\varphi(\theta, \hat{\theta}) = \begin{cases} v(\theta) \left[\Phi_1^F \left(\frac{v(\hat{\theta})}{V_1^F} \right) + q_M(F_2, M_2) \pi(\omega(c_1(\hat{\theta}), \theta)) \right] & \text{for } \theta \in [\theta_{\min}, \bar{\theta}_1] \\ v(\theta) \left[1 + q_M(F_2, M_2) \pi(\omega(c_1(\hat{\theta}), \theta)) \right] & \text{for } \theta \in [\bar{\theta}_1, \theta_{\max}] \end{cases}.$$

A male will choose the “best” possible value of $\hat{\theta}$: the value of $\hat{\theta}$ such that $\frac{\partial \varphi(\theta, \hat{\theta})}{\partial \hat{\theta}} = 0$:

$$\begin{cases} \frac{v(\theta)}{V_1^F} \Phi_1^F \left(\frac{v(\hat{\theta})}{V_1^F} \right) v'(\hat{\theta}) + q_M(\cdot) v(\theta) \pi'(\omega(c_1(\hat{\theta}), \theta)) \omega_c(c_1(\hat{\theta}), \theta) c_1'(\hat{\theta}) = 0 & \text{for } \theta \in [\theta_{\min}, \bar{\theta}_1] \\ q_M(\cdot) v(\theta) \pi'(\omega(c_1(\hat{\theta}), \theta)) \omega_c(c_1(\hat{\theta}), \theta) c_1'(\hat{\theta}) = 0 & \text{for } \theta \in [\bar{\theta}_1, \theta_{\max}] \end{cases}. \quad (11)$$

By the second line, $c_1(\theta)$ is constant for $\theta \in [\bar{\theta}_1, \theta_{\max}]$, yielding utility:

$$U(\theta) = v(\theta) [1 + q_M(F_2, M_2) \pi(\omega(c(\bar{\theta}_1), \theta))] \quad \text{for } \theta \in [\bar{\theta}_1, \theta_{\max}].$$

By continuity, the value of the constant value of the signal is $c(\bar{\theta}_1)$. Consider now $\theta \in [\theta_{\min}, \bar{\theta}_1]$. Differentiate (8) with respect to θ :

$$\begin{aligned} \dot{U}(\theta) = & v(\theta) \left[\frac{v'(\theta)}{V_1^F} \Phi_1^F \left(\frac{v(\theta)}{V_1^F} \right) + q_M(\cdot) \pi'(\omega(c_1(\theta), \theta)) \omega_c(c_1(\theta), \theta) c_1'(\theta) \right] \\ & + v'(\theta) \left[\Phi_1^F \left(\frac{v(\theta)}{V_1^F} \right) + q_M(\cdot) \pi(\omega(c_1(\theta), \theta)) \right] \\ & + v(\theta) q_M(\cdot) \pi'(\omega(c_1(\theta), \theta)) \omega_\theta(c_1(\theta), \theta). \end{aligned}$$

Incentive compatibility implies $\frac{\partial \varphi(\theta, \hat{\theta})}{\partial \hat{\theta}} \Big|_{\theta=\hat{\theta}} = 0$, and so, by (11), the first term in the above vanishes, thus establishing (9). Consider (10): $c_1(\theta)$ must be strictly monotonic,

in order for the females to be able to “invert” it and infer θ from c . Clearly it cannot be decreasing: if the cost of signal decreased with θ , each male would have an incentive to choose the signal associated with the best type, $c_1(\theta_{\max})$: not only he would be mistaken for the highest type male, but would also have the lowest cost of signalling. Finally, for $\theta \in [\bar{\theta}_1, \theta_{\max}]$, the last part of the statement, notice that there is no point in increasing the signal beyond the level that induces every female to mate, and males of higher type than $\bar{\theta}_1$ will therefore not separate. ■

We can now solve the problem with optimal control techniques, (Leonard and van Long 1992, LvL hereafter).¹⁸ The state variable is $U(\theta)$, and $c_1(\theta)$ is the control variable. $U(\bar{\theta}_1)$ is free, and the lower boundary condition is given by the requirement that the lowest type does not advertise, obtaining payoff:

$$U(\theta_{\min}) = v(\theta_{\min}) \Phi_1^F \left(\frac{v(\theta_{\min})}{V_1^F} \right) + \frac{F_2}{M_2} v(\theta_{\min}) \pi(\omega(0, \theta_{\min})). \quad (12)$$

The problem can therefore be stated formally as an optimal control problem, with a free terminal “time” $\bar{\theta}_1$, a scrap value function, – the second integral in the maximand (13) – (LvL pp 244ff), and control parameters M_2, F_2, V_1^F (LvL pp 253ff):

$$\max_{\substack{c_1(\theta), M_2, \\ F_2, V_1^F}} \int_{\theta_{\min}}^{\bar{\theta}_1} U(\theta) \phi_1^M(\theta) d\theta + \int_{\bar{\theta}_1}^{\theta_{\max}} v(\theta) \left[1 + \frac{F_2}{M_2} \pi(\omega(c(\bar{\theta}_1), \theta)) \right] \phi_1^M(\theta) d\theta, \quad (13)$$

s.t. (4), (6), (7), (9) and (10).

To state the main result succinctly, define the function:

$$a(c, w, \theta) = \frac{f_{\theta c}(c, w, \theta)}{f_c(c, w, \theta)} - \left(\frac{\pi''(w)}{\pi'(w)} + \frac{f_{wc}(c, w, \theta)}{f_c(c, w, \theta)} \right) \frac{f_{\theta}(c, w, \theta)}{f_w(c, w, \theta)}.$$

Assumption 1 For every $(c, w, \theta) \in C \times W \times [\theta_{\min}, \theta_{\max}]$, let

$$a(c, w, \theta) + \frac{v'(\theta)}{v(\theta)} \geq 0, \quad (14)$$

and let $a_{\theta}(c, w, \theta) \leq 0$ and $a_c(c, w, \theta) > 0$.

Proposition 4 If Assumption 1 holds, then there is a solution to problem (13).

¹⁸Grafen (1990) determines the equilibrium using functional analysis, and Bergstrom et al (2002) propose an approach based on vector field analysis. As far as I am aware, there are no approaches using optimal control.

Proof. To apply optimal control solution methods, the integral constraints (4) and (7) need to be replaced by auxiliary constraints and state variables (LvL p 191). Write (7) as:

$$\int_{\theta_{\min}}^{\bar{\theta}_1} v(\theta) \pi(\omega(c_1(\theta), \theta)) \phi_1^M(\theta) d\theta = \frac{M_2 V_1^F}{q_M(F_2, M_2)} - \int_{\bar{\theta}_1}^{\theta_{\max}} v(\theta) \pi(\omega(c(\bar{\theta}_1), \theta)) \phi_1^M(\theta) d\theta,$$

and replace it with:

$$\begin{aligned} \dot{k}(\theta) &= v(\theta) \pi(\omega(c_1(\theta), \theta)) \phi_1^M(\theta), \\ k(\theta_{\min}) &= 0, \quad k(\bar{\theta}_1) = \frac{M_2 V_1^F}{q_M(F_2, M_2)} - \int_{\bar{\theta}_1}^{\theta_{\max}} v(\theta) \pi(\omega(c(\bar{\theta}_1), \theta)) \phi_1^M(\theta) d\theta. \end{aligned} \quad (15)$$

Similarly for (4), which is replaced by:

$$\begin{aligned} \dot{h}(\theta) &= \pi(\omega(c_1(\theta), \theta)) \phi_1^M(\theta), \\ h(\theta_{\min}) &= 0, \quad h(\bar{\theta}_1) = M_2 - \int_{\bar{\theta}_1}^{\theta_{\max}} \pi(\omega(c(\bar{\theta}_1), \theta)) \phi_1^M(\theta) d\theta. \end{aligned} \quad (16)$$

The Lagrangean associated to problem (13) can now be written as:

$$\begin{aligned} \mathcal{L} &= U(\theta) \phi_1^M(\theta) d\theta + \\ &+ \mu(\theta) \left\{ v'(\theta) \Phi_1^F\left(\frac{v(\theta)}{V_1^F}\right) + q_M(F_2, M_2) [v(\theta) \pi'(\omega(c_1(\theta), \theta)) \omega_\theta(c_1(\theta), \theta) \right. \\ &+ v'(\theta) \pi(\omega(c_1(\theta), \theta))] \left. \right\} + \xi(\theta) v(\theta) \pi(\omega(c_1(\theta), \theta)) \phi_1^M(\theta) \\ &+ \zeta(\theta) \pi(\omega(c_1(\theta), \theta)) \phi_1^M(\theta) + \lambda \left[F_2 - \int_0^1 \delta \Phi_1^M(\max\{v^{-1}(\delta V_1^F), \theta_{\min}\}) \phi_1^F(\delta) d\delta \right], \end{aligned} \quad (17)$$

where $\xi(\theta)$ and $\zeta(\theta)$ are the Pontryagin multipliers associated to constraint (9), (15) and (16), and λ the Lagrange multiplier associated to constraint (6) (LvL p 255). To determine the costate variable $\mu(\theta)$, differentiate \mathcal{L} with respect to $U(\theta)$.

$$-\frac{\partial \mathcal{L}}{\partial U(\theta)} = \dot{\mu}(\theta) = -\phi_1^M(\theta).$$

Solving the above with the boundary conditions $\mu(\bar{\theta}_1) = 0$ (because $U(\bar{\theta}_1)$ is free), and $\mu(\theta_{\min})$ free (LvL Theorem 7.1.1, p 222), gives:

$$\mu(\theta) = \Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta).$$

The multipliers for the transformed integral constraints are:

$$\begin{aligned} -\frac{\partial \mathcal{L}}{\partial k(\theta)} &= \dot{\xi}(\theta) = 0, & \xi \text{ constant,} \\ -\frac{\partial \mathcal{L}}{\partial h(\theta)} &= \dot{\zeta}(\theta) = 0, & \zeta \text{ constant.} \end{aligned}$$

Notice that ξ and ζ are both positive: they increase the value of the Lagrangean (17), and can be interpreted as the shadow prices (LvL p 152ff) of M_2 and V_1^F , an increase

in both of which increase males' payoff. Now, $c_1(\theta)$, which must satisfy the condition $\frac{\partial \mathcal{L}}{\partial c_1(\theta)} = 0$. Expanding it and re-arranging gives:

$$v(\theta) [\pi''(\cdot) \omega_\theta(\cdot) \omega_c(\cdot) + \pi'(\cdot) \omega_{\theta c}(\cdot)] + \pi'(\cdot) \omega_c(\cdot) \left(v'(\theta) + \frac{\phi_1^M(\theta)(\xi v(\theta) + \zeta)}{[\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)] q_M(F_2, M_2)} \right) = 0,$$

$$\frac{\pi''(\cdot)}{\pi'(\cdot)} \omega_\theta(\cdot) + \frac{\omega_{\theta c}(\cdot)}{\omega_c(\cdot)} + \left(\frac{v'(\theta)}{v(\theta)} + \frac{\frac{\phi_1^M(\theta)}{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)}}{q_M(F_2, M_2)} \left(\xi + \frac{\zeta}{v(\theta)} \right) \right) = 0. \quad (18)$$

The terms in $\omega(\cdot)$ can be replaced using the following result.

Lemma 3 $\omega_c(\cdot) = -\frac{f_c(\cdot)}{f_w(\cdot)} < 0$, $\omega_\theta(\cdot) = -\frac{f_\theta(\cdot)}{f_w(\cdot)} > 0$, $\omega_{c\theta}(\cdot) = -\frac{f_{\theta c}(\cdot) f_w(\cdot) - f_{w c}(\cdot) f_\theta(\cdot)}{f_w(\cdot)^2}$.

Proof. Start from total differentiation of $f(c, w, \theta) = 0$, to get $f_c(\cdot) dc + f_w(\cdot) dw + f_\theta(\cdot) d\theta = 0$. And $\omega_c = \frac{dw}{dc}$, and so on. ■

And so (18) becomes:

$$a(c_1(\theta), w, \theta) + \left(\frac{v'(\theta)}{v(\theta)} + \frac{\frac{\phi_1^M(\theta)}{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)}}{q_M(F_2, M_2)} \left(\xi + \frac{\zeta}{v(\theta)} \right) \right) = 0. \quad (19)$$

Now notice that, since $a_c(\cdot) > 0$, $c_1(\theta)$ can be obtained from (19) as a function where F_2 , M_2 , V_1^F , and $\bar{\theta}_1$, and the multipliers ξ and ζ are parameters. This can be substituted for $c_1(\theta)$ in the appropriate constraints and first order conditions, and solved. This is conceptually simple, but algebraically complex, and I do not do it here. In order for the expression $c_1(\theta)$ derived from (19) to be a feasible solution, it is also necessary that it is strictly increasing, in $[\theta_{\min}, \bar{\theta}_1]$ (see (10)). The derivative with respect to θ of the term in the large brackets in (19) is:

$$\frac{v''(\theta)}{v(\theta)} - \left(\frac{v'(\theta)}{v(\theta)} \right)^2 + \frac{\frac{d}{d\theta} \left(\frac{\frac{\phi_1^M(\theta)}{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)}}{q_M(F_2, M_2)} \left(\xi + \frac{\zeta}{v(\theta)} \right) \right) - \frac{\frac{\phi_1^M(\theta)}{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)} \frac{\zeta v'(\theta)}{v(\theta)^2}}{q_M(F_2, M_2)}}{q_M(F_2, M_2)}. \quad (20)$$

Rewrite (19) as

$$\xi + \frac{\zeta}{v(\theta)} = -\frac{q_M(F_2, M_2) \left(a(c, w, \theta) + \frac{v'(\theta)}{v(\theta)} \right)}{\frac{\phi_1^M(\theta)}{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)}},$$

and so (20) can be written as :

$$A = \frac{v''(\theta)}{v(\theta)} - \left(\frac{v'(\theta)}{v(\theta)} \right)^2 - \frac{\frac{d}{d\theta} \left(\frac{\frac{\phi_1^M(\theta)}{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)}}{q_M(F_2, M_2)} \left(\xi + \frac{\zeta}{v(\theta)} \right) \right)}{\frac{\phi_1^M(\theta)}{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)}} \left[a(c, w, \theta) + \frac{v'(\theta)}{v(\theta)} \right] \quad (21)$$

$$- \frac{\frac{\phi_1^M(\theta)}{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)} \frac{\zeta v'(\theta)}{v(\theta)^2}}{q_M(F_2, M_2)}.$$

If (14) holds, then the term in the square bracket is positive and so the third term is negative. The other terms are all negative: recall that $\frac{d}{d\theta} \left(\frac{\Phi_1^M(\bar{\theta}_1) - \Phi_1^M(\theta)}{\phi_1^M(\theta)} \right) < 0$, and so the derivative of the reciprocal is positive, $v'(\theta) > 0$, $v''(\theta) < 0$, and $\zeta, \xi > 0$. Therefore A is itself negative. Next totally differentiate (19) with respect to θ and c :

$$a_c(c, w, \theta) dc + [a_\theta(c, w, \theta) + A] d\theta = 0,$$

and so

$$\frac{dc_1}{d\theta} = \frac{-a_\theta(c, w, \theta) - A}{a_c(c, w, \theta)}.$$

By the assumptions in the statement, A is negative, see (21), $a_\theta(c, w, \theta) < 0$ and $a_c(c, w, \theta) > 0$, and therefore $\frac{dc_1}{d\theta} > 0$, which ends the proof. ■

5 Utility maximisation.

Living species subject to evolutionary pressure reach a point on the trade-off between survival and reproduction which maximises fitness subject to their environmental constraints.¹⁹ The “preferred” loudness of the courtship call of a male frog of a given size balances subtly the caller’s chances of attracting females and attracting frog eating bats (Ryan et al 1982). A biologist could therefore, in theory at least, derive frogs’ preference for loudness from the observation of the environment where frogs live: in terms of the model described above, from the knowledge of the functions $f(c, w, \theta)$ and $\pi(w)$. With the exceptions of the works cited in footnote 1, economists do not generally derive preference, assuming them instead, without considering whether their assumptions are consistent with an evolutionary viewpoint (Grafen 1998).

I show in this section that the standard economic problem of maximising utility from consumption subject to a budget constraint, and the biological problem of the maximisation of fitness subject to environmental constraints are formally equivalent. This provides an evolutionary foundation for maximisation of a utility function with consumption vectors as arguments.

I consider the two-period case examined in Section 4, using an argument which proceeds in three steps; the extension to the T -period case is conceptually analogous. In the first step I construct a correspondence between the males’ trade-off between survival and reproduction and their trade-off between

¹⁹Fitness is a slippery concept in biology, see Dawkins 1982, pp 179–194. In this paper, however, in the absence of “altruistic” interaction between individuals, individual “inclusive fitness” and the population genetics concept of frequency of the genotype in the population coincide; they both correspond to Becker’s use of the concept of “genetic fitness” (1976).

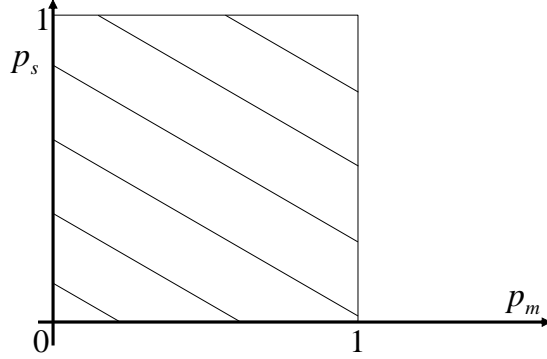


Figure 2: Isopayoff loci in the (p_m, p_s) -cartesian space.

consumption goods. I then derive the males' utility function. This is fully determined by the environment, which includes the behaviour of the females of the species. Moreover, it is independent of θ : the preferences of individuals with different θ can be represented by the same utility function. In the third and final step I establish the correspondence between the solutions of the two problems.

Step 1. Consider an individual facing two independent lotteries. In the first lottery, mating, with probability $p_m \in [0, 1]$ he mates, obtaining a number of – average quality – descendants $v(\theta)$, and with the complement probability, $1 - p_m$, he does not mate, which gives a 0 payoff. The second lottery is survival, which happens with probability $p_s \in [0, 1]$ and gives payoff $q_M(F_2, M_2)v(\theta)$ and again 0 in the event of death. Total expected payoff is therefore:

$$v(\theta)(p_m + q_M(F_2, M_2)p_s). \quad (22)$$

Consider next the space $[\theta_{\min}, \theta_{\max}] \times W$. A point on this space represents the pair of the individual type θ and his acquisition of survival assets w . Let the probability space $[0, 1]^2$ and the space $[\theta_{\min}, \theta_{\max}] \times W$ be linked by the function $G : [\theta_{\min}, \theta_{\max}] \times W \rightarrow [0, 1]^2$, which associates to a point (θ, w) the probabilities of mating and of surviving for a male of type θ who has survival consumption w .

$$G : (\theta, w) \mapsto \left(\Phi_1^F \left(\frac{v(\theta)}{V_1^F} \right), \pi(w) \right).$$

The function G depends on the population distribution in the equilibrium, via the parameter V_1^F . Notice also that G is one-to-one, and therefore invertible, in $[\theta_{\min}, \bar{\theta}_1] \times W$.

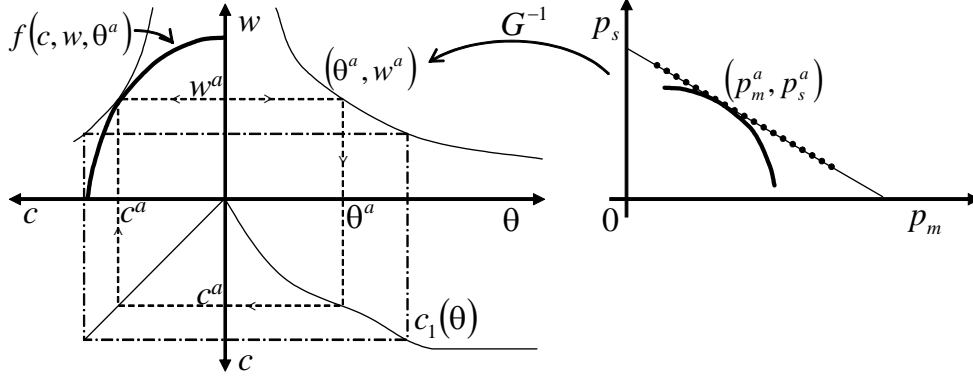


Figure 3: Indifference curve and constraint in the (c, w) -cartesian space.

Step 2. Consider the locus

$$I_k = \left\{ p_m, p_s \in [0, 1]^2 \mid v(\theta) (p_m + q_M (F_2, M_2) p_s) = k \right\}.$$

This is the locus of the points representing combination of probabilities which give the same payoff. These are straight lines with slope $-q_M (F_2, M_2)$, depicted in Figure 2, in the (p_m, p_s) cartesian space, for various values of k .

Consider the space of consumption vectors $C \times W$, where a point $(c, w) \in C \times W$ represents a combination of conspicuous consumption (with no survival value) and survival consumption. The function G can be used to construct indifference curves in the consumption space (c, w) as follows. Start from a locus I_k , and apply G^{-1} to each point in $I_k \cap G([\theta_{\min}, \bar{\theta}_1] \times W)$. This is the set of points that gives payoff k and are in the range of G where G is invertible, say the points on the dotted line on the RHS of Figure 3. The image of these points under G^{-1} is the locus on the north east quadrant of the LHS of the diagram: for example, point (p_m^a, p_s^a) is mapped into point $(\theta^a, w^a) = G^{-1}(p_m^a, p_s^a) = \left(\Phi_1^F \left(\frac{v(\theta^a)}{V_1^F} \right), \pi(w^a) \right)$.

The points on the curve $G^{-1}(I_k \cap G([\theta_{\min}, \bar{\theta}_1] \times W))$ represent combinations of type θ and survival consumption w which give the same payoff. Now simply transfer this curve to the $C \times W$ space by writing $c_1^{-1}(c)$ instead of θ :

$$w = w(c) = \pi^{-1} \left(\frac{\frac{k}{v(c_1^{-1}(c))} - \Phi_1^F \left(\frac{v(c_1^{-1}(c))}{V_1^F} \right)}{q_M (F_2, M_2)} \right). \quad (23)$$

(23) is the indifference curve between c and w . Diagrammatically, the optimal strategy $c_1(\theta)$ derived in Section 4 takes a point (θ^a, w^a) in the north-east quadrant to the corresponding point in the north-west quadrant. From θ^a , follow the dashed curve clockwise to the south east quadrant, which shows the locus $c_1(\theta)$ derived in the previous section, then to south-west quadrant, which has a 45 degree line, and determines the abscissa c^a corresponding to the ordinate θ^a in the north-west quadrant. Repeating the procedure for every point in the set $I_k \cap G([\theta_{\min}, \bar{\theta}_1] \times W)$ gives the points (c^a, w^a) which, given the strategies of all members of the population, yield a male the same payoff. The dash-dot line maps another point on the iso-payoff curve. Clearly it is not necessarily the case that these points are feasible or optimal. A standard indifference curve, for goods which are both valuable, the image of the set $I_k \cap G([\theta_{\min}, \bar{\theta}_1] \times W)$ must be downward sloping. This is established in the following Lemma.

Lemma 4 *If Assumption 1 holds, then the image of $I_k \cap G([\theta_{\min}, \bar{\theta}_1] \times W)$ onto the (c, w) cartesian space is a decreasing function.*

Proof. Since Assumption 1 holds, $c_1(\theta)$ is increasing, and, therefore, it is sufficient to show that the image of $I_k \cap G([\theta_{\min}, \bar{\theta}_1] \times W)$ under G^{-1} onto the (θ, w) cartesian space is a decreasing function. To establish this, note that, be on the I_k locus, a point (θ, w) must satisfy

$$v(\theta) \left(\Phi_1^F \left(\frac{v(\theta)}{V_1^F} \right) + q_M(F_2, M_2) \pi(w) \right) = k.$$

Rearrange to get

$$w = \pi^{-1} \left(\frac{\frac{k}{v(\theta)} - \Phi_1^F \left(\frac{v(\theta)}{V_1^F} \right)}{q_M(F_2, M_2)} \right);$$

differentiate with respect to θ :

$$w = -\frac{\pi^{-1'}(\cdot) v'(\theta)}{q_M(F_2, M_2)} \left(\frac{k}{v(\theta)^2} + \frac{\phi_1^F \left(\frac{v(\theta)}{V_1^F} \right)}{V_1^F} \right) < 0.$$

■

Note that the indifference curves identify a preference relation on (c, w) in the standard Arrow-Debreu sense, and the utility function is constructed by assigning a numerical value to each indifference class, $u(c, w)$. The utility function is invariant to strictly monotonic transformation, and, moreover, is the same for all male's types θ . It does depend on the function $c_1(\theta)$; this, as far as each given male is concerned, is of course part of the environment.

Step 3. The standard consumer's problem is

$$\max_{c,w} u(c, w), \quad \text{s.t.: } f(c, w, \theta) = 0. \quad (24)$$

We can transfer the points on this locus by repeating the procedure described in Step 2 in the opposite direction. This maps the constraint from the space $C \times W$ to the space of lotteries $[0, 1]^2$. Take a value of $\theta \in [\theta_{\min}, c^{-1}(c_{\max})]$, say θ^a . This determines a constraint $f(c, w, \theta^a)$, depicted in the north-west diagram as the thick black line,²⁰ and mapped into the north-east diagram as the set of points $c_1^{-1}(c), \omega(c_1^{-1}(c), \bar{\theta})$ (not shown). Applying G to this set, and the thick curve in the RHS of the diagram is obtained. This is the set of points satisfying:

$$(p_m, p_s) = G(c_1^{-1}(c), \omega(c_1^{-1}(c), \theta^a)) = \left(\Phi_1^F \left(\frac{v(c_1^{-1}(c))}{V_1^F} \right), \pi(\omega(c_1^{-1}(c), \theta^a)) \right). \quad (25)$$

Consider the problem of choosing the optimal trade-off between the survival and the reproduction lottery.

$$\max_{p_m, p_s} v(\theta) \left(p_m + \frac{F_2}{M_2} p_s \right), \quad \text{s.t.: (25)}. \quad (26)$$

In order to have a well defined utility maximisation problem (and hence a well defined fitness maximisation biology problem), the constraint must lie below the indifference curve. On the RHS diagram, this is simply the requirement that the image of the constraint be concave, as depicted. The relevant condition is given in Proposition 5.

Proposition 5 *If*

$$\left(\frac{f_{cc}(\cdot)}{f_c(\cdot)} - \frac{f_{cw}(\cdot)}{f_w(\cdot)} - \frac{\pi''(\cdot) f_c(\cdot)}{\pi'(\cdot) f_w(\cdot)} \right) - \left(\frac{\phi_1^{F'}(\cdot)}{\phi_1^F(\cdot)} v'^{-1}(\cdot) + \frac{v''(\cdot)}{v'(\cdot)} \right) < 0,$$

then there is an internal solution to problem (26), which is mapped by G^{-1} into the solution to problem (24).

Proof. An interior solution exists if $\frac{d^2 p_s}{d p_m^2} < 0$. (25) is a locus parameterised by c . To derive its slope, take the derivative of both p_s and p_m with respect to c .

$$\frac{d p_s}{d p_m} = \frac{\pi'(\omega(c_1^{-1}(c), \theta^a)) \omega(c_1^{-1}(c), \theta^a)}{\phi_1^F \left(\frac{v(c_1^{-1}(c))}{V_1^F} \right) \frac{v'(c_1^{-1}(c))}{V_1^F}}. \quad (27)$$

²⁰By construction, it touches the indifference curve at point $(c_1(\theta), w)$.

Invert the first component of (25) $c = c_1 \left(v^{-1} \left(V_1^F \Phi_1^{F-1} (p_m) \right) \right)$ and substitute this value into (27):

$$\frac{dp_s}{dp_m} = V_1^F \frac{\pi' \left(\omega \left(v^{-1} \left(V_1^F \Phi_1^{F-1} (p_m) \right), \theta^a \right) \right) \omega_c \left(v^{-1} \left(V_1^F \Phi_1^{F-1} (p_m) \right), \theta^a \right)}{\phi_1^F \left(\Phi_1^{F-1} (p_m) \right) v' \left(v^{-1} \left(V_1^F \Phi_1^{F-1} (p_m) \right) \right)}.$$

Differentiate the above with respect to p_m and re-arrange to obtain:

$$\frac{d^2 p_s}{dp_m^2} = \frac{\pi'(\cdot) \omega_c(\cdot) v^{-1'}(\cdot) V_1^F \frac{d\Phi_1^{F-1}(p_m)}{dp_m}}{\phi_1^F(\cdot) v'(\cdot)} \left\{ \left[\frac{\pi''(\cdot)}{\pi'(\cdot)} \omega_c(\cdot) + \frac{\omega_{cc}(\cdot)}{\omega_c(\cdot)} \right] - \left[\frac{\phi_1^{F'}(\cdot)}{\phi_1^F(\cdot)} v'^{-1}(\cdot) + \frac{v''(\cdot)}{v'(\cdot)} \right] \right\}.$$

Apply Lemma 3 to determine that the above is negative if and only if the condition given in the Lemma is satisfied. ■

As before, the point of these conditions is not so much their plausibility or interpretability, but rather the fact that they could be violated or satisfied, implying that whether a given species' biology problem is equivalent to a utility maximisation problem depends in general on exogenous circumstances.

6 Concluding remarks

This paper views utility maximisation as a consequence of evolutionary pressure exerted by sexual selection. It ends with some empirical evidence, necessarily somewhat heuristic in nature, and with the interpretation in the light of the ideas proposed here of some aspects of human behaviour that economists have typically found difficult to reconcile with the standard optimising model.

6.1 Resources and signalling.

Murdock and White (1969) dataset contains information on around 200 “pre-industrial” human societies, where conditions and behaviours are more likely to resemble those prevailing at the time our psychological traits took shape. The necessarily approximate nature of this dataset, and the relative lack of economic variables restrict its use in economics, and while certainly unsuitable for a rigorous test of the conditions in Assumption 1, which depend on the shape of the constraint $f(c, w, \theta)$, the survival function $\pi(w)$, and the benefit function $v(\theta)$ in a non-linear way, it allows nevertheless a simple test of the link between resources and signalling. In my model, if resources are barely sufficient for survival, then signalling is prohibitively expensive, and hence unlikely to emerge as a viable equilibrium strategy. I account for the interaction

between female choice and the benefit of signalling via a stylised model where the exogenously given society resources affect the degree of polygyny (more resources allow a more unequal distribution of resources and hence of females), and where signalling is beneficial to the extent that females exert choice. Polygyny, *ceteris paribus*, increases the benefit of signalling. To estimate this,²¹ I construct indices of how polyginous a society is (the variable “polygyny” in the equations below), and of how close it is to subsistence (the variable “resources”, containing, among others, the development and the reliance on agriculture, the quality of the environment, including diseases, the extent of female contribution to subsistence, the frequency of famines and starvation). Signalling (“signal”) is measured by the presence of activities, such as mining, woodcarving, hunting large game, musical instruments and so on, which are not necessary for survival, and whether these activities are carried out by men or by women; “female choice” measures how necessary a woman’s agreement is for her to be married. A two stage least square estimation of simultaneous equations, to account for the endogeneity of polygyny, gives the following results (161 observations are used, *t*-statistics are in brackets, and the Pseudo R^2 are 0.09 and 0.20):

$$\text{polygyny} = .337 + .338 \text{ resources} - .101 \text{ pop. density}$$

(2.64) (3.84) (2.56)

$$\text{signal} = 1.59 + .205 \text{ polygyny} + .136 \text{ female choice} - .265 \log(\text{population})$$

(5.63) (1.82) (2.63) (4.69)

The coefficients in these equations have the predicted signs: more resources entail more polygyny, and more female choice increase the likelihood that signalling is taking place in the society. Coefficients are significant at the 5% level with the exception of the polygyny index in the second equation, which is significant at 10%. Population size and density also influence the endogenous variables; the use of different exogenous variables does not alter the qualitative nature of the estimation, indicating, within the limits of the dataset, a certain robustness of the results.

6.2 Conspicuous consumption in the Pleistocene.

Kohn and Mithen’s (1999) theory that handaxes were the product of sexual selection also suggests support for my paper. Handaxes are very intriguing ar-

²¹Details are available on request or at www.le.ac.uk/economics/gdf4/curres.htm

chaeological finds: manufactured for over one million years, they are frequently found *unused* in very large hoards in individual sites, perfected well beyond the necessity of use, their very symmetry and size making many of them inappropriate for any practical purpose such as throwing or butchering. All these features induce Kohn and Mithen to reject the “survival” justification of such a persistent oddity, and to opt instead for a sexual selection explanation: the ability to knap and handle symmetric and polished handaxes was used as reliable indicator of a potential mate’s quality by those of the opposite sex, and thus conferred a reproductive advantage which outweighed the survival costs involved in their production, the time diverted from feeding or hunting while looking for materials and knapping, the risk of injury to hands and eyes, and so on.²²

Viewing sexual selection as a powerful engine for evolution can help biologists explain the development of certain traits which would provide little or no survival value unless fully developed. A classic example is the evolution from reptiles’ scales to birds’ feathers: light and flimsy scales have lower survival value than either solid scales or fully formed feathers, so it is difficult to explain what drove evolution from the former to the latter, given that evolution does not plan for the long term. Sexual selection can indicate a possible route. If the flimsiness and lightness of an individual’s scales serve as a costly signal (since flimsy and light scales are less useful as a defence mechanism) reptiles with flimsier and lighter scales, would visibly signal their unobservable characteristics. Eventually this sexually selected trait also proved to have survival advantages, and become further established and developed. If we translate this argument to humans, we can address one of the Darwin’s puzzles of human evolution, the development of mental abilities with little or no survival value at the time they evolved. In the spirit of Miller (2000), my paper can be interpreted to suggest that dexterity, manufacturing, understanding of the relative merits of different materials, knowledge of the sources of such materials, mining, and so on, all developed as a means of impressing the members of the opposite sex and influencing their mating choices, and were continually improved by sexual selection, until the time where the level of development reached by these traits

²²It is also worth noting that the unobserved characteristic of interest to females which is signalled is single dimensional, the contribution to fitness of offspring. Therefore, a single dimensional signal is sufficient, and this might also explain the exclusive reliance on handaxes, which appear to have been the only item which was manufactured on the planet for a very long period of time: the explosion in tools use and variety occurred around 50,000 years ago.

would also have a survival value, in manufacturing sharper spears, in selecting and mining suitable materials and so on.²³

The arbitrariness of sexually selected traits may also prompt the question of possible alternative routes that human evolution might have taken. One conceivable example is information gathering and processing: what if, at the dawn of the human race, our ancestors had considered the most desirable mates those with the best ability to recognise remember and classify features of the environment such as leaves in trees, animal footprints, birds flights, star configurations, weather patterns, rather than those with the most conspicuous consumption? Clearly a signal of this nature would soon acquire a large potential survival value, and might lead to many imaginable different human evolutionary paths beginning there. The exploration of this possibility is however best left to science fiction writers.

6.3 Sex differences

Sexually selected traits differ in the two sexes; the view proposed in this paper receives therefore an indirect confirmation from the differences observed in the general attitude of men and women towards consumption. Few nowadays question the evolutionary psychologists' view that there are profound differences between the sexes (eg Buss 1994 and 2004): not only in the attitudes towards casual and extramarital sex, which has a direct explanation in terms of differential parental investment, and justifies the assumption in the model that men and women have different attitudes towards multiple mating in the season, but also in the attitudes towards wealth and resources. From warfare, which is typically waged by men, and it is almost universally caused by the quest for more territory and resources,²⁴ to the observations that men value earnings and possessions more than women do, that they are more systematic collectors than women, and that men with more resources have more sexual partners (Kanazawa 2003), and more attractive partners, to Buss's team's results, who systematically analysed lonely hearts columns and conducted surveys in 37 different societies, amply demonstrating how women prefer wealth in men, when men prefer youth (Buss *et al.* 1990), the mass of evidence accumulated in this

²³Other traits, such as the aesthetic sense or the ability to judge the symmetry of a manfact also developed but did not have a survival value. Miller (2000) extends this argument to include the development of many specifically human activities such as art, music, conversation, arts, humour and so on.

²⁴Both in human and in chimpanzees, the only other species in which it is known that bands of males set out to attack other males from a different group (Buss 2004, pp 280ff.)

respect overwhelmingly supports the claim that “men seek wealth because they know it attracts women” (Ridley 2003, p 54). And in order to perform this function, wealth must be displayed, and in our forebears’ environment, conspicuous consumption was one of the few effective ways to display one’s wealth.

6.4 Altruism

Most people leave tips in restaurants which they will never visit again; by the same token, overwhelming experimental evidence indicates that subjects playing ultimatum or dictator games do not take advantage of other players who are complete strangers, and will remain so at the conclusion of the experiment. Many of the explanations for this *prima facie* irrational behaviour are based on some form of maladaptation (see Samuelson 2005, pp 96–100): Seabright suggests that a tendency not to take advantage of short term opportunities evolved at a time when essentially all interactions happened within a group. There has therefore been no opportunity for a darwinian evolution of the ability to distinguish between members of the group, co-operation towards whom does have a long term evolutionary advantage, and strangers, who will not be met again, and there is no such advantage (2004, p 61-62). Similarly, we should not “be surprised if the physiological and psychological mechanisms that have evolved to sustain equilibria in repeated games should somehow be triggered inappropriately in one-shot situations”, such as anonymous experimental ultimatum games (Binmore 1994, p 183). Frank’s view (1987), on the other hand, is not based on maladaptation: altruist individuals enjoyed an evolutionary advantage, as they could be trusted in cooperative ventures, which exceeded the short term cost of altruistic acts. According to Frank, emotions have evolved both as a signal and as a commitment device: feeling guilty if we cheat someone, be they strangers or friends, reduces the utility of selfishly taking advantage of short term opportunities.

In addition to the survival advantages which “genes for altruism” may confer to their human bearers, this paper suggests that there may also have been strong reproductive benefits accruing to individuals who behaved altruistically: consumption is meant to be displayed to convert it into mating opportunities, and, in an environment where long-lasting physical commodities are rare, “acts of altruism” may serve as a substitute for durable stores of value. By increasing c , an act of altruism serves as a signal that one is accumulating enough resources that the cost of “wasting” some on strangers is negligible. A recent example is

the potlatch, a ceremonial feast in some Native American population in which chiefs ostentatiously destroy wealth (similar events occur in New Guinea, and among the Maori, the Koha, the Kula, the Moka): “the potlatch consists of goods that are perishable or vulnerable; the prestige that it buys is a good that is durable and portable” (Ridley 1986, p 122).

This viewpoint may shed light on some altruistic acts which are inconsistent with standard explanations: for example, in restaurants, men tip better than women, and men accompanied by women tip better than men alone and than men accompanied by other men (Miller 2000, p 326); similarly, men are more likely to give to street beggars if they are walking with a woman (Stark 1992). The interpretation that men try to impress women with their altruism runs into the obvious difficulty that from a woman’s survival perspective what matters is her partner’s altruism *towards her*; acts of altruism towards strangers are in fact bad news, because they indicate a propensity to profligacy which would divert resources away from her and their offspring. If, however, as contended here, altruism is a form of consumption, then it acts as a costly signal of a man’s unobservable qualities, and it make perfect sense that it should be practised more when it is more likely to be observed by females.

This argument, incidentally, is in line with the conclusion that Zahavi and his associates have drawn following their decades long observation of the Arabian babblers (*Turdoides squamiceps*), a small bird living in groups in the Israeli deserts. They are altruistic: they share “chick care”, they put their lives at greater risk by acting as sentinels for the group and mobbing predators, they share food with non-relatives. A repeated game justification based on Trivers’ (1985) concept of reciprocal altruism would predict that these birds would try to cheat when they can get away undetected, reaping benefits without paying the costs. In fact, they do nothing of the sort: they *compete* to perform the apparently altruistic acts: dominant birds, upon seeing a subordinate trying to act as sentinel, will attack and drive off the subordinate, taking over the sentinel role; they try forcibly to stuff food down the throats of reluctant non-relatives. The Zahavis propose they are using these ‘altruistic’ acts as handicaps to display their fitness, thereby attaining better reproductive prospects within the group. “The helper benefits from the act of helping, and *the benefits to others are incidental*” (Zahavi and Zahavi 1997, p 134, my emphasis).

6.5 The endowment effect.

Consider, to end, the “endowment effect” (Thaler 1980): people require more to be separated from an object they own than they are willing to pay for the same object when they do not own it. The experimental evidence, which is inconsistent with traditional explanations based on transaction costs or income effects, has been interpreted in support of the theory of reference dependent utility (Kahneman et al. 1990). A different, not necessarily alternative, explanation is suggested by the analysis of this paper. To the extent that possession of physical goods is a signal, utility should be increased by the possession of visible goods more than by the right to receive the same goods, because, while today this right is represented by money, with a high certainty of conversion, in the Pleistocene, when our utility function took shape, the conversion of promises into goods was likely to be less than certain, and so having a claim to a good was not the same as possessing the good itself. In a variant of the experiment which seems designed to test this idea, instead of exchanging money for goods, experimental subjects traded money for tokens that represented a claim to those same goods. In this case, there was no observed endowment effect: subjects had the same trade-off to receive and to give up tokens. This clearly tallies with the ideas of this paper, once it is noted that tokens and money have the same signal value, which is lower than the signal value displayed by physical possession of the goods.

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