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Sexual selection, conspicuous consumption and economic growth

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Abstract We propose that the evolution by sexual selection of the male propensity to engage in conspicuous consumption contributed to the emergence of modern rates of economic growth. We develop a model in which males engage in conspicuous consumption to send an honest signal of their quality to females. Females prefer males who express the costly and honest signal, leading males who engage in conspicuous consumption to have higher reproductive success than those who do not, increasing the prevalence of signalling males in the population. As males fund their conspicuous consumption through participation in the labour force, an increase in the prevalence of signalling males gives rise to an increase in economic activity that leads to economic growth.

1 Introduction

In the majority of species, females invest more into offspring than males. Females produce costly eggs instead of cheap sperm, invest substantial amounts of resources

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into offspring during pregnancy or provide extensive brood care of young. Consequently, females are choosy and prefer males who give them or their offspring fitness enhancing benefits (Trivers 1972). This forces males to compete for access to females, often resulting in large differences in reproductive success between males relative to that between females (Bateman 1948; Wade 1979). The resulting sexual selection can generate rapid genetic and phenotypic change in a population (Maynard Smith 1978; Andersson 1994).

Males have evolved a range of traits that are advantageous when competing with rival males for access to females. This includes extravagant traits that are costly for the bearer, such as the plumage of peacocks, the bright coloration of butterflies or ornamental morphological structures such as the antlers of deer (Zahavi 1975). By imposing a cost or handicap on the male that cannot be borne by males with limited abilities or resources, these secondary sexual characteristics can provide an honest signal of underlying quality to the female (Grafen 1990a, b). As such signals are honest, females benefit if they prefer males who give signals, while the increase in mating opportunities compensates the males for the cost of the signal.

Sexual selection has been an important force in human evolution, as emphasized by Darwin (1871). The higher variance in reproductive success for men than for women (Fisher 1930; Brown et al. 2009) is suggestive of the struggle between males for mating opportunities with females. Using estimates of genetic diversity from a range of studies, Wade and Shuster (2004) estimated that sexual selection accounts for about half of total selection in *Homo sapiens*. Accordingly, men have evolved secondary sexual characteristics to signal their quality, which include behavioural traits such as the propensity to engage in conspicuous consumption (Frank 1999; Miller 1999, 2001; Saad 2007).

Since Veblen's (1899) identification of the preference for conspicuous consumption, conspicuous consumption has been recognized as a social phenomenon relevant to economic analysis. However, economic models typically ascribe no evolutionary foundation for consumption. From an evolutionary perspective, high consumption will only persist if it increases the fitness of the agent relative to those who consume less. Thus, an assumption that people seek to maximise consumption can only hold if maximising consumption enhances fitness. De Fraja (2009) addressed this problem by providing an evolutionary foundation to the economic hypothesis that humans seek to maximise consumption. Using a modified version of Grafen's (1990a, b) models on biological signals as handicaps, he demonstrated that conspicuous consumption could be explained as an honest signal of male quality.

This paper extends previous analyses of the evolutionary foundations of conspicuous consumption by examining conspicuous consumption in a dynamic evolutionary framework. Our goal is to extend the work of De Fraja (2009) by moving from a steady state population equilibrium analysis to an examination of the dynamic evolution of the trait and its economic effects. This makes it necessary to extend the analysis to include the interaction between reproductive success, conspicuous consumption and economic activity.

In our model some males carry a gene that predisposes them to signal their quality through engaging in conspicuous consumption, while others do not. Conspicuous consumption might involve autonomous activities such as developing art or other objects

of beauty in traditional societies, or participating in the labour force to earn income in modern times. The definition of conspicuous consumption should be considered to be broad, and to include any consumption activities beyond those required for survival. The female's receptivity to male conspicuous consumption results in males being under strong selection to express the trait, which increases the prevalence of the gene underlying the behaviour and the level of conspicuous consumption in the population.

To fund conspicuous consumption, a male must participate in activities to obtain the resources to consume, which reduces the time available for subsistence and therefore the probability of survival. Males will only signal through conspicuous consumption if the fitness benefits through increased mating opportunity outweigh the handicap of lower survival probability. We show that a separating equilibrium exists in which signalling males increase in prevalence, with the female preference for high-quality males who signal through conspicuous consumption compensating for the survival cost of the signal.

We propose that this increase in conspicuous consumption increases economic growth through two avenues: increased labour engaged in productive uses to acquire resources to conspicuously consume, and a scale effect (Romer 1990; Kremer 1993) whereby the level of human capital engaged in production drives technological progress. As an illustration, handaxes have been observed at archaeological sites at frequencies and levels of symmetry far above that required for purely for survival. Kohn and Mithen (1999) proposed that these handaxes were the products of sexual selection, with the ability to manufacture highly symmetrical handaxes a reliable indicator of the quality of the maker. As such, progress in stone tools was partly driven by competition for mates. As a modern example, a male must engage in high-value activities in the labour force to acquire sufficient wealth to purchase discretionary consumer items, which might range from fashionable clothes to a sports car. Their labour effort and any innovation they exercise to acquire these goods contribute to economic activity. Further, the production of many of these goods for conspicuous consumption involves high levels of innovation, such as through precision engineering.

As female mating choice increases male conspicuous consumption and the level of economic activities to fund it, we propose that sexual selection was a contributing factor to the emergence of modern levels of economic growth. As such, the model provides a basis for the observation that males engage in work effort and consumption at levels above that required for survival (or at the cost of survival) and proposes that these behaviours have substantial economic effects.

2 Related literature

Over the last 40 years, a range of economic preferences of humans has been examined in an evolutionary context. This includes the evolution of altruism (Becker 1976; Hirshleifer 1977), risk preferences (Rubin and Paul II 1979), and time preference (Hansson and Stuart 1990; Rogers 1994; Robson and Samuelson 2007; Robson and Szentes 2008; Netzer 2009; Robson and Samuelson 2009).

More recently, a growing literature deals with the link between the evolutionary dynamics of these traits and economic growth. In a seminal paper, Galor and Moav

(2002) proposed that changes in prevalence of a genetically based preference for quality or quantity of children were a trigger for the Industrial Revolution. Galor and Michalopoulos (2012) argued that selection for a genetically determined entrepreneurial spirit (proxied by risk aversion) could be the cause of modern levels of economic growth. In these papers, selection is ecological, being based on survival due to availability of resources above a subsistence level and allocation of those resources to children.

Zak and Park (2002) incorporated sexual selection into a model of economic growth as part of a broader analysis of gene-environment interactions and their economic effects. In their agent-based model, female choice affects the evolution of cognitive ability, as females prefer smarter males. Sexual selection may explain the observation of Clark (2007) that fertility was higher among wealthy men in the lead-up to the Industrial Revolution. He proposed that the fecundity of well-off families increased the proportion of the population with the preferences and habits conducive to economic progress. Clark's findings match other evidence of higher reproductive success of men with more resources, particularly in hunter-gatherer societies and among pastoralists (Mulder 1987, 1990; Cronk 1991; Hopcroft 2006). Although the link between resources and reproductive success may have weakened in recent times, positive sexual selection on male income has been observed in contemporary Sweden, Britain and the United States (Nettle and Pollet 2008).

Conspicuous consumption is likely to have deep evolutionary roots. Evidence of conspicuous consumption dates back to the development of stone axes, with many axes constructed to a degree of specification beyond that required for practical use, or at a cost to practical use (Kohn and Mithen 1999). Trade in shell beads has been dated to over 80,000 years ago (Bouzouggar et al. 2007), and the prevalence of monument building across cultures is also suggestive of a propensity to conspicuously consume (for example, Neiman 1997). Recent research in evolutionary psychology has linked conspicuous consumption with mating displays. Griskevicius et al. (2007) found that men who are shown photos of women or who read a romantic scenario were more willing to spend on luxuries than men who were exposed to neutral images. Sundie et al. (2011) showed that men looking for short-term partners wished to spend more on conspicuous consumption when primed with mating scenarios. Women asked to rate two otherwise identical men preferred the owner of a luxury car as a short-term partner. Yet, men showed no response to female conspicuous consumption.

3 Model with evolution of male preference

3.1 The agents

The model comprises a population of male and female agents who live for one mating season. The number of males and females at the start of generation t, $M(t)$ and $F(t)$, are normalised to a constant level such that $M(t) = M(t + 1)$ and $F(t) = F(t + 1)$. For ease of notation, the indicator t relating to the generation is omitted except where a distinction is required to be made between two generations.

Males vary in inherent quality ($0 < h^k \leq 1$), which is allocated randomly at birth. We assume that males can be of high ($k = H$) or low ($k = L$) quality with probability p and $1 - p$. The assumption of random allocation of quality allows the evolution of conspicuous consumption to be analysed without conflating the analysis with inherited changes in the agents' qualitative traits.

The agents are haploid: that is, a single gene codes for each trait. Each male has one genetic locus, with the allele (variant of the gene) at that locus expressing for signalling behaviour. There are two alleles that determine the agents' set of actions, signalling (S) and not signalling (N), which are transmitted directly from father to son. The frequency of each male phenotype in the population is denoted by π^{ik} ($i \in S, N; k \in H, L$). For example, π^{SH} indicates the frequency of high-quality signalling males in the population. $\pi^i = \pi^{iH} + \pi^{iL}$ denotes the prevalence of males of type i of either level of quality.

As humans are diploid, this haploid arrangement can be thought of as representing the inheritance of a phenotypic characteristic between generations, with the alleles standing for the different phenotypes. Abstraction of this nature is common in modelling the evolution of social behaviour in humans as it avoids complications presented by diploid reproduction, genetic interactions and multi-gene traits (Grafen 1991). Where the genetics underlying the trait of interest are not understood and the area of interest is the selective force on the expressed trait, the assumption of haploidy provides a convenient way of modelling the evolution of phenotypic traits. This arrangement could also be thought of as vertical transmission of a cultural trait, where the son learns the signalling behaviour from his father.

The utility of a male is defined as the number of children he fathers. The male utility function can only be defined in terms of the particular model details, so is given below in Eqs. (20) and (21) after the model is further specified. The male utility function is only a correlate of fitness, as fitness is maximised if the number of viable offspring in the long-term is maximised. The single-generation form of the utility function is adopted through this paper for mathematical tractability. However, in this version of the model, a male's decision to maximise offspring numbers in the next generation is equivalent to long-term fitness maximisation, as the male cannot affect the genotype or quality of his children.

Female agents are identical and are passive, except for their mating decision. Females prefer males of higher quality, as the number of surviving children, n, is an increasing function of the quality of the male with whom she mates.

$$n = n\left(h^k\right) \quad n_h\left(h^k\right) > 0 \tag{1}$$

The utility of a female depends on the number of surviving children.

$$u^F = n\left(h^k\right) \tag{2}$$

As for the male, the female utility function is not a direct statement of the female's long-term fitness. She cares about the genotype of the male with whom she mates, as the genotype of her child will affect that child's reproductive success and that of future

generations. However, in a separating equilibrium, the single-generation form of the female utility function is still fitness maximising, with the choice of utility function affecting only the condition under which a separating equilibrium occurs. The change to this condition is discussed in further detail below.

Females are assumed to have an innate preference for observing male signals and, as they cannot directly observe male quality, use male conspicuous consumption as a proxy in the mating decision. The assumption that females cannot directly observe a dimension of quality is supported by the ubiquity of costly signalling behaviour in humans (Miller 2001). The innate preference of females reflects a situation where male evolution is shaped by a pre-existing female sensory bias (Basolo 1990; Ryan 1990, 1998; Miller 2001). Rather than male and female behaviour co-evolving, here the female preference is a fixed trait that does not evolve.[1]

3.2 The economy

The economy consists of two sectors: the subsistence sector and the luxury sector. The subsistence sector comprises activities that increase the probability of agent survival, such as hunting, gathering and resting. The luxury sector comprises labour market activities to access a surplus with which to engage in conspicuous consumption. In early evolutionary times before a modern division of labour, luxury sector activities might have involved conspicuous leisure (Veblen 1899), production of art or ornaments (such as symmetrical handaxes), body ornamentation or other costly displays of underlying quality (Miller 2001). When the development of agriculture allowed greater specialisation, time engaged in the luxury sector expanded to include specialised production activities and ultimately participation in the modern labour force.

Production in each sector uses inputs of labour and a scarce environmental factor, such as land, whose quantity we fix and normalise to one. Males have one unit of time that they allocate between the subsistence and luxury sectors. The proportion of time that a male is engaged in subsistence activities is s^{ik}, with the remaining time, $1 - s^{ik}$, spent in the luxury sector. Only males who carry the signalling allele S allocate time to the luxury sector and engage in conspicuous consumption. Thus, non-signalling males spend all their time in the subsistence sector ($s^{Nk} = 1$).

Each agent has an equal share of the fixed factor, giving each agent $1/M$ of the fixed factor, where M is the number of males. Agents allocate their use of the fixed factor between sectors in the same proportions as they do their time.

Agents receive the product of their own subsistence sector and luxury sector labour. Effective labour input in the luxury sector is a function of both the time allocated to labour activity in that sector and the quality of that agent. Accordingly, each agent receives income in the subsistence sector, z^{ik}, and luxury sector, c^{ik}, as follows:

$$z^{ik} = A^S \left(s^{ik}\right)^\rho \left(\frac{s^{ik}}{M}\right)^{1-\rho} = A^S s^{ik} M^{\rho-1} \quad \rho \in (0, 1) \tag{3}$$

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[1] Male-female coevolution is explored in the electronic supplementary material.

$$c^{ik} = A^L \left(1 - s^{ik}\right)^\alpha h^{ik} \left(\frac{1 - s^{ik}}{M}\right)^{1-\alpha} = A^L \left(1 - s^{ik}\right) h^{ik} M^{\alpha-1} \quad \alpha \in (0, 1) \quad (4)$$

The parameters ρ and α are the elasticity of output with respect to labour input in each sector. The shift factors A^S and A^L are the level of technology in the subsistence sector and luxury sector.

Aggregate output, Y, is given by the sum of output in the subsistence sector and the luxury sector.

$$Y = \sum_{i=S,N} \sum_{k=H,L} \pi^{ik} \left(A^S s^{ik} M^\rho + A^L \left(1 - s^{ik}\right) h^{ik} M^\alpha\right) \tag{5}$$

Under Eqs. (3) and (4), the wage per unit of labour in the subsistence sector, r^{ik}, and the wage per efficiency unit of labour in the luxury sector, w^{ik}, are:

$$r = A^S M^{\rho-1} \tag{6}$$
$$w = A^L M^{\alpha-1} \tag{7}$$

In a given sector, all agents receive the same wage per unit or efficiency unit of labour because the production technology exhibits constant returns to scale and they invest the same proportion of the fixed factor in each sector, as they do their labour.

As the wage in the luxury sector is per efficiency unit, low-quality males will receive a lower wage per unit of time engaged in the luxury sector than high-quality males. Therefore, low-quality males face a higher effective cost for conspicuous consumption, raising their cost of signalling. Signalling males are subject to the following budget constraint.

$$c^{ik} \leq w h^k \left(1 - s^{ik}\right) \tag{8}$$

We assume that the subsistence sector has zero technological progress and set A^S to one. In a Malthusian economy, technological progress would be matched with population growth, effectively constraining income growth. As the population is normalised to a fixed level for each generation, the assumption of zero technological progress in the subsistence sector allows for maintenance of a Malthusian environment without introducing population growth into the model.

The level of technology in the luxury sector is determined endogenously in the model. It is assumed that technological progress, g, is an increasing and concave function of the number of efficiency units of labour engaged in the luxury sector, L. This is similar to the scale effect as a driver of technological progress in Romer (1990), in which technological progress is a function of the human capital engaged in research, or Kremer (1993), who assumed that technological progress is a function of population size.

The number of efficiency units of labour engaged in the luxury sector is given in Eq. (9), with the function for technological progress given in Eq. (10).

$$L = M \sum_{i=S,N} \sum_{k=H,L} \pi^{ik}(1 - s^{ik})h^k \tag{9}$$

$$g = \frac{A(t+1) - A(t)}{A(t)} = g(L, A^L)$$

$$g_L > 0 \quad g_{LL} \le 0 \quad g\left(0, A^L\right) = 0 \tag{10}$$

3.3 The mating season

Each generation lives for one mating season, which comprises three stages denoted by A, B and C. The mating season can be thought of as one of a series of short-term partnerships, as a sequence of "serial monogamy" during a lifetime, or (in the case of some agents) as a complete monogamous life. In stage A males work and in stages B and C mating takes place. In this section we describe how males and females move from stage A to B to C in the mating season.

Equal numbers of males and females are born and enter stage A ($M_A = F_A$). Males suffer from pre-breeding mortality in stage A. Male survival probability, δ^{ik}, is a function of their subsistence income relative to a minimum subsistence level of income, $\bar{z}$.

$$\delta^{ik} = \delta\left(z^{ik}, \bar{z}\right) \quad \delta_z\left(z^{ik}, \bar{z}\right) > 0 \quad \delta_{zz}\left(z^{ik}, \bar{z}\right) \le 0$$

$$\delta\left(0, \bar{z}\right) = 0 \quad \delta\left(r, \bar{z}\right) \le 1 \tag{11}$$

The number of surviving males who are available to mate in stage B is:

$$M_B = \sum_{i=S,N} \sum_{k=H,L} \pi_A^{ik} \delta^{ik} M_A \tag{12}$$

As male mortality is not uniform, the prevalence of males of each type in stage B varies from that in stage A:

$$\pi_B^{ik} = \pi_A^{ik} \delta^{ik} \frac{M_A}{M_B} \tag{13}$$

The number of females does not change from stage A to B as there is no female mortality ($F_B = F_A$).

In stages B and C, males and females are randomly paired and the female chooses whether to mate with the male. As males are polygynous and make no investment in the offspring, they can mate in both periods. Females can mate only once, as they must make a maternal investment in their children. While this paper has two mating periods, the results can be generalised to more than two mating periods.

The probability of a male or female being matched depends on the number of males and females in the mating pool. In stage B, the probability of being matched is one for
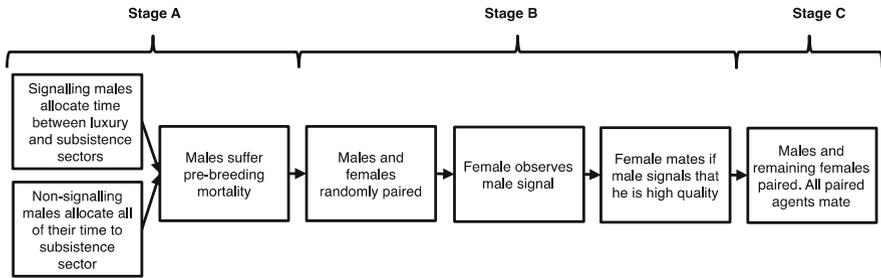
Fig. 1 The mating season

a male $\left[q_B^M = q(M_B, F_B) = 1\right]$, as male mortality ensures that there are fewer males than females. The probability of being matched for a female is:

$$q_B^F = q(M_B, F_B) = \frac{M_B}{F_B} = \sum_{i=S,N} \sum_{k=H,L} \pi_A^{ik} \delta^{ik} \tag{14}$$

When a female is paired in stage B, she decides whether she will mate with the male. If she does, the female exits the mating pool and gives birth to that male's children. A male always agrees to mate with the female he is matched with, as there is no cost to mating for a male.

There is no further mortality of males after stage A. The number of males and the ratio of types of males do not change between stages B and C ($M_C = M_B$ and $\pi_C^{ik} = \pi_B^{ik}$). The number of females available for mating in stage C comprises the females who did not mate in stage B.

Depending on male mortality in stage A and the frequency of mating acceptance by females in stage B, it is possible for males and females to be unmatched until stage C, which is the final breeding period. A female's probability of being matched in stage C, q_C^F, will be greater than the corresponding probability in stage B as some females mate and exit the mating pool in stage B, whereas the number of available males remains constant.

$$q_C^M = q(M_C, F_C) = \min\left\{1, \frac{F_C}{M_C}\right\} \tag{15}$$

$$q_C^F = q(M_C, F_C) = \min\left\{1, \frac{M_C}{F_C}\right\} \tag{16}$$

In stage C, both females and males will mate with whomever they are matched with as females will have no further opportunities to mate and mating for males does not involve a cost. Offspring from the mating in stages B and C are then born and form the next generation. The mating season is summarised in Figure 1. Females observe male signals after they are randomly paired with males in stage B. There is no male signalling in stage C as females will accept any male they are matched with.

3.4 Female optimisation

The female decision whether to agree to mate with a given male is a binary decision: yes or no. A female will mate in stage B if the benefit is greater than the benefit she expects to receive from mating in stage C. As the female is unable to distinguish between a high-quality non-signalling male and a low-quality male, she must weight the expected quality of the male with whom she is paired in stage B against expected future quality in stage C. She will reject a non-signalling male in stage B if:

$$E\left[n(h^k)\right] \le q_C^F \sum_{i=S,N} \sum_{k=H,L} \pi_C^{ik} n\left(h^k\right) \tag{17}$$

If all remaining females are paired in stage C, this condition will always be met as $q_C^F = 1$ and $n\left(h^L\right) < n\left(h^H\right)$. Equation (17) is always satisfied unless there is a low probability of a female being paired with a male in stage C. This might occur if male mortality rates were high in stage A and few females mate in stage B.

If the female utility function were an exact representation of fitness, females would also weight the probability that the male is of the signalling genotype. The absence of a signal in stage B, in addition to signifying that the male is potentially of low quality, could mean that the male is of a non-signalling genotype. As signalling males have higher fitness in a separating equilibrium, this increases the incentive of the female to delay mating until stage C. This makes a separating equilibrium more likely. Once this separating equilibrium occurs, the mating decision of the female is identical regardless of whether the utility function is strictly a statement of long-term fitness. Females mate only with high-quality males who signal in stage B.

As a female observes conspicuous consumption rather than male quality, the mating decision of the female depends on whether the level of conspicuous consumption is sufficient, with the threshold level denoted by $\bar{c}$.

$$\theta\left(c^{ik}\right) = \begin{cases} 0 & if\ c^{ik} \le \bar{c} \\ 1 & if\ c^{ik} > \bar{c} \end{cases} \tag{18}$$

If Eq. (17) is not satisfied, a female will set $\bar{c}$ at a level that will only be achieved by high-quality males. In that case, we can state the number of females available to mate in stage C as:

$$F_C = \left(1 - q_B^F \pi_B^{SH}\right) F_B \tag{19}$$

In this specification of the model, a female who delays her mating decision incurs no cost to the delay beyond the small probability of not being paired in stage C. The model could incorporate costs to delay such as a probability of death before the second mating period [as was included in the model by De Fraja (2009)] or by recognising the increased relative fertility inherent with a shorter time between generations.

3.5 Male optimisation

The male's utility function can now be stated. The number of children fathered by a male is a function of his survival probability, whether a female accepts him as a mating partner, and the male's quality. Survival probability and mating success are a function of the level of conspicuous consumption. If females only mate with high-quality signalling males in stage B, the signalling and non-signalling males vary in the manner in which they optimise the number of children. Their respective utility functions are:

$$u^{Sk} = \delta^{Sk} \left(\theta q_B^M + q_C^M \right) n \left(h^k \right) \tag{20}$$

$$u^{Nk} = \delta^{Nk} q_C^M n \left(h^k \right) \tag{21}$$

Substituting the budget equation (8) into Eqs. (20) and (21), a male of each type faces the following optimisation problem:

$$\left\{ s^{Sk} \right\} = argmax \left\{ \delta^{Sk} \left(rs^{Sk}, \bar{z} \right) \left[\theta \left(wh^k \left(1 - s^{Sk} \right) \right) q_B^M + q_C^M \right] n \left(h^k \right) \right\} \tag{22}$$

$$\left\{ s^{Nk} \right\} = argmax \left\{ \delta^{Nk} \left(rs^{Nk}, \bar{z} \right) q_C^M n \left(h^k \right) \right\} \tag{23}$$

If females will not mate with non-signalling males in stage B [i.e. Eq. (17) is satisfied], high-quality signalling males will maximise utility by signalling if the gain from the additional mating opportunity in stage B [the left-hand side of Eq. (24)] exceeds the decreased mating opportunity due to the increased probability of death (the right hand side).

$$\delta^{SH} q_B^M \geq \left(\delta^{NH} - \delta^{SH} \right) q_C^M \tag{24}$$

If there were more than two mating periods, the required decrease in survival probability before the high-quality signalling males would have lower fitness would be even greater. This condition is easier to satisfy if $M_C > F_C$, as the reduced probability of being paired in stage C makes the opportunity to pair in stage B relatively more important.

Finally, the non-signalling and low-quality males spend all of their time on survival activities ($s^{SL} = s^{Nk} = 1$).

3.6 Offspring

Offspring are born and raised at the end of the mating season. Assuming the females accept the high-quality males who signal, the offspring born from mating in stage B, who all inherit the signalling allele, are:

$$n_B^S = \pi_A^{SH} \delta^{SH} n(h^H) M_A \tag{25}$$

The mating during stage C results in offspring of both genotypes:

$$n_C^i = \sum_{k=H,L} \pi_C^{ik} n\left(h^k\right) \min\{M_C, F_C\} \tag{26}$$

The number of offspring born in each stage determines the prevalence of each genotype in the next generation. The prevalence of the signalling genotype in generation $t + 1$ is:

$$\pi_A^S(t+1) = \frac{n_B^S + n_C^S}{n_B^S + n_C^S + n_C^N}$$

$$= \pi\left(p, \pi_A^S, h^{L,}h^H\right) \tag{27}$$

As the population is normalised to a constant level at the start of the next generation, Eq. (27) gives the relative proportion of each genotype in total population $M(t)$.

The prevalence of the signalling type in the population increases if $\pi_A^S(t+1) > \pi_A^S(t)$. Using this condition, Eq. (27) can be used to derive Eq. (24), which determines whether high-quality males signal and mate in stage B. This shows that the signalling allele increases in prevalence if condition (24) is met.

3.7 Signalling equilibrium

As shown by Grafen (1990a, b), the core condition for the emergence of a separating equilibrium on the basis of a signalling handicap is that the signallers of different quality experience different costs (or benefits) to their signalling behaviour.[2] The low-quality male must experience greater costs (or lower benefits) for the same size signal as that produced by a high-quality signaller.

In our model, the cost of signalling to a male is the reduction in offspring due to the lower probability of survival associated with a signal of size c. The cost can be derived from Eqs. (8) and (11), and is weighted by the probability of being paired in stage C.

$$Cost = q_C^M \left[\delta(r, \bar{z}) - \delta\left(r\left[1 - \frac{c}{wh^k}\right], \bar{z}\right)\right] \tag{28}$$

The cost of conspicuous consumption of level c is larger for the low-quality male as they receive a lower wage for their labour and must sacrifice a greater quantity of subsistence activity to match a high-quality male's signal.

The benefit of conspicuous consumption is the expected increase in children due to the signal. The benefit of signalling is equal to the probability of surviving to stage B, being paired and the female allowing the male to mate with her. The benefit can be derived from Eqs. (11) and (18). The benefit depends negatively on signal strength c as the increasing probability of death reduces the weighted benefit of the additional mating opportunity.

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[2] Spence (1973) observed the requirement of differential cost for an honest signal in his analysis of job signaling markets.

$$Benefit = q_B^M \theta \delta \left(r \left[1 - \frac{c}{wh^k} \right], \bar{z} \right) \qquad (29)$$

Adding the costs and benefits together in Eqs. (28) and (29) gives us the condition in which males are willing to signal in Eq. (24).

There is a range of signal strength that a high-quality male is willing to make that a low-quality male will not match as the cost is above the mating benefit. If a low-quality male is willing to set conspicuous consumption at or below c^*, whereas a high-quality male is prepared to signal up to a level of c', conspicuous consumption in the interval c^* to c' gives an honest signal of male fitness. Accordingly, females set the threshold level $\bar{c}$ for the signal above c^*. High-quality males have first mover advantage as they set the signal before the female decides whether to mate. Therefore, high-quality males will signal at the level (or an infinitesimal amount above) that low-quality males are indifferent about. In other words, high-quality males will set the signal just above c^*.

In a separating equilibrium, no-one has an incentive to deviate. If high-quality males signal at a higher level, they reduce their survival for no mating gain. A lower signal size would be copied by low quality males, resulting in no mating benefit as females cannot trust the signal. Low-quality males will not copy a signal above c^*, as its cost exceeds its benefit to them. Females will not raise their threshold level of acceptance as they would then miss the opportunity to mate with high-quality males, while a reduction in threshold would make signalling attractive to low-quality males.

3.8 Model dynamics

When Eqs. (17) and (24) are satisfied, there will be a separating equilibrium where high-quality males signal and females consent to mate in stage B only if paired with one of those high-quality signalling males. In a separating equilibrium, the prevalence of the signalling allele in the population will increase because the reproductive success of the signalling males will be higher than that for non-signalling high-quality males. This will in turn increase labour force participation in the luxury sector and the rate of technological progress, driving an increase in income and economic growth.

The per generation percentage point change in the prevalence of the signalling allele is:

$$\Delta \pi^S = \frac{p \pi_A^S \left(1 - \pi_A^S \right) \left[\left(1 + q_C^M \right) \delta^{SH} - q_C^M \delta^{NH} \right] n \left(h^H \right)}{p \pi_A^S \delta^{SH} n \left(h^H \right) + q_C^M \sum_{i=S,N} \sum_{k=H,L} \pi_A^{ik} \delta^{ik} n \left(h^k \right)} \qquad (30)$$

The term $\pi_A^S (1 - \pi_A^S)$ in the numerator shows the frequency dependent nature of the change in the prevalence of the signalling allele. At low frequencies of the signalling allele, there are few signallers who experience reproductive success, and at high frequencies the rate slows as the prevalence approaches the upper bound of 100 per cent.

The rate of change, $\Delta \pi^S$, increases with the proportion of the population that is high quality, p, as an increased prevalence of high-quality males results in more males indicating the presence of the signalling allele through signalling. The rate of change also increases with the difference in reproductive success between high and

low-quality males, $n(h^H)$ and $n(h^L)$, as the high-quality signalling males obtain a relatively greater benefit from their mating success.

According to Eq. (24), the term $(1 + q_C^M)\delta^{SH} - q_C^M \delta^{NH}$ in the numerator of Eq. (30) is positive. An increase in this term increases the selection rate through the greater relative benefit of signalling. $1 + q_C^M$ depends on the number of mating periods in a season, with high-quality signalling males having $1 + q_C^M$ expected mating opportunities, compared to the q_C^M opportunities of the other types. If there were more than two mating periods in a season, the signalling allele would spread more quickly as signalling males would have even more opportunities to attract a mate. The survival rates of the signallers and non-signallers, δ^{ik}, are also relevant, with more costly signalling slowing the spread of the signalling allele. The size of the required signal is, however, likely to fall as the survival cost increases, reducing the effect of changes in survival probability on the spread of the allele.

The increase in the prevalence of signalling males increases economic growth in two ways. First, labour participation in the luxury sector increases. This increase in work effort is reflected in the historical record. Reviewing a number of studies, Voth (2000) notes that the average hours worked per day increased from an average of 4.9 h in hunter-gatherer communities, to 7.4 in mixed communities and to 10.9 h per day in advanced sedentary agricultural societies The second way that signalling males contribute to economic growth is through technological progress. As technological progress is a function of the population engaged in the labour force, technological progress increases with the increase in the prevalence of signalling males.

The electronic supplementary material provides a simulation to illustrate the dynamics of the model under a plausible set of parameters. The take-off in economic activity is robust to changes in parameter values, and is largely a function of the two mating periods per mating season. More than two mating periods in a season would increase the rate of evolutionary change by giving signalling males more opportunities to mate. Sensitivity testing of parameters relating to the relative fertility of low and high-quality types and the prevalence of high-quality males suggests that the spread of the signalling allele and associated increase in economic activity could occur in tens to hundreds of generations.

The electronic supplementary material also contains a second model in which both male and female behaviour is determined genetically. Depending on their type, female agents observe the male signal and use that information to infer quality, or they ignore the signal. As a result, male and female signalling and observing behaviour must co-evolve, rather than male signalling behaviour exploiting an existing female sensory bias as occurred in the above model. In that case, the co-evolution of the male and female traits results in longer-term trend in economic growth and it takes hundreds to thousands of generations for the signalling trait to spread through the population.

4 Discussion

The hypothesis presented in this paper is that sexual selection was a contributing factor to the emergence of modern levels of economic growth. As females prefer males who conspicuously consume, males are under selection to increase their allocation

of time to innovation, labour and other productive activities in order to engage in conspicuous consumption. These activities contribute to technological progress and economic growth.

The core condition for an honest signal such as conspicuous consumption is different costs (or benefits) of signalling between high and low-quality signallers. In our model, the difference in costs to signalling arises from the difference in wages that each high and low-quality male can earn in the luxury sector of the economy for purchasing conspicuous consumption goods. Even if there was no such wage difference, the necessary condition for existence of a handicap as an honest signal could have been met through alternative means. The model could be reframed so that high and low-quality males face different costs of decreased investment into subsistence activities, with the survival probability for low-quality males declining faster. The increased survival cost faced by a low-quality male would allow a separating equilibrium. If we assumed that the "quality" trait affected multiple outcomes, including survival probability and labour efficiency, the condition for the handicap would be met in multiple dimensions.

In our model, sexual selection does not affect the quality of the agents. Quality is allocated randomly at birth, which made the model tractable for an analysis of the handicap principle. If quality were heritable, selection of high-quality individuals would tend to drive the genes associated with high quality to fixation, at which point female choice would become obsolete. A more realistic but complicated scenario would be to introduce multiple genes associated with quality and allow selection and mutation of these genes to occur. This would allow female choice to remain important, while allowing qualitative population changes to occur. We consider that this scenario would be more representative of the human evolutionary history, with the propensity for conspicuous consumption and qualitative traits both being selected for in the population.

In addition to being a signal of quality, conspicuous consumption may be a signal of accumulated resources, which are likely to be of value to a female. Female interest in resource accumulation is likely to play a significant role in the evolution of a preference for conspicuous consumption. In the models in this paper, agents do not accumulate resources as there is no capital and no transmission of resources from males to females. The ability to accumulate resources may change the inherent trade-offs between quality and signalling ability, particularly if resources can be transmitted to children.

If capital accumulation were incorporated into the model, the effect of conspicuous consumption on capital accumulation may create an ambiguous effect on growth, particularly in modern economies. The lower savings rate implied by higher conspicuous consumption may reduce long-term growth as there is less accumulated capital for productive uses. However, capital investment is itself likely be driven by the desire for conspicuous consumption, which is increased over the long-term through the return on that capital. The preference for conspicuous consumption provides an incentive to invest in resources that will generate income in excess of that required for survival.

One omission from our model is the positive effect on survival of the activities undertaken to support conspicuous consumption. The labour and innovation of previous centuries has not only improved the methods to acquire resources for conspicuous

consumption, but has also affected basic survival probability. In advanced economies, survival to adulthood is likely with probability above 99 per cent (Department of Economic and Social Affairs 2011). Once conspicuous consumption imposes no cost on the individual, it loses its reliability as a signal. Accordingly, we might expect the nature of conspicuous consumption to change in modern contexts, or for alternative methods of signalling to emerge. However, if the preference for conspicuous consumption is a heritable trait, females may still prefer conspicuous consumption despite its diminished usefulness as a signal. This trait would persist in the population until the preference for signals that are more accurate spread.

This is not to say, however, that conspicuous consumption can have no survival cost today. Conspicuous consumption also occurs in poor societies, often at significant cost to the signallers. Moav and Neeman (2012) theorised that conspicuous consumption is more prevalent in poor societies than in societies with higher income, as in advanced economics people can signal through career, qualifications or other costly methods of demonstrating quality.

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