

**TRUTHFUL SIGNALLING,
THE HERITABILITY PARADOX, AND THE
MALTHUSIAN EQUI-MARGINAL PRINCIPLE**

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ABSTRACT

The article shows that heritable quality differentials are consistent with the Zahavi Handicap Principle (the Truthful Signalling Hypothesis). Earlier analyses have assumed non-heritable quality. The crucial innovation is the Malthusian Equi-Marginal Principle: under selection pressures the relative numbers of higher and lower-quality organisms will change until, in equilibrium, not the average but the marginal levels of quality will be equalized. Each male maximizes his own reproductive success and signals until the marginal value of more signaling is zero. We further require evolutionary stability; displacements to higher or lower population sizes must be restored to equilibrium. The article proposes an alternative to Fisher's (1929) and Hamilton and Zuk's (1982) suggestions. The model is solvable for ranges of parameters that constitute the stable region. We particularly consider the unit signalling costs of the high-quality and low-quality males, where it has been widely believed that for a TSH equilibrium the former must be lower than the latter. This article confirms our earlier result that this is not a necessary condition for a truthful signalling equilibrium, though the unit signalling costs of the high quality males cannot be too much larger.

Keywords: Heredity, Signalling, mating competition, general equilibrium, handicap principle, Malthusian equi-marginal principle.

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1. Introduction

In an early passage of *The Handicap Principle* (1997, p. xv), Amotz and Avishag Zahavi describe the initially adverse reception of their idea: “When we first suggested this Handicap Principle in 1975 it was almost unanimously rejected.” But the tide turned with the publication of two logically complete papers by Alan Grafen (Grafen 1990a, 1990b). Actually, owing to their high degree of mathematical abstraction, most readers must have taken the Grafen articles on faith as demonstrating the internal logical consistency of the Zahavi Handicap Principle. (Or, as we will usually term it, the Truthful Signalling Hypothesis.) But, building upon Grafen’s work, the present authors (Hausken and Hirshleifer, 2004) have generated, by a direct and reproducible instantiation applying functional forms, a logically complete analytical system and solution consistent with the Truthful Signalling Hypothesis. This method generates easily reproducible results. So the question of the internal logical consistency of the Handicap Principle has been resolved.¹ However, this “happy ending” is not complete. The Grafen and the Hausken and Hirshleifer analyses were both based upon an artificial premise, that the quality differentials forming the basis for handicap signalling were non-heritable. To wit, that the quality differentials forming the basis for handicap signalling were non-heritable. “In the first stage, males are randomly assigned a quality independently of their genotype ...” – Grafen (1990a, p. 475).

A number of readers and analysts, perhaps even the great majority, seem unaware that Grafen’s analysis dealt only with non-heritable quality. Thus Dawkins: “Quality, for Grafen, means that ... females would benefit genetically [sic!] if they mated with good males ...” (Dawkins, 1989, p. 310). Of course, females cannot benefit genetically if the good males do not differ genetically from the inferior males. And Zahavi and Zahavi themselves (1997, p. 58), while also claiming support from Grafen’s demonstration, associate handicap signals with a range of male quality traits many of which—indeed, almost all of those described in their book – are clearly heritable. As an exception, Noldeke and Samuelson (2001) have noticed the limitation of Grafen’s analysis to non-heritable quality variation.

So, since the main concern of biologists is surely with heritable quality rather than or in addition to non-heritable quality, the question is really still open. Is the Handicap Principle, or Truthful Signalling Hypothesis, valid – in the sense of internal logical consistency – when the quality

¹Getty (2005) argues that the resulting internally consistent system does not correspond to a sports handicapping system, and that the metaphor is not externally valid because better quality individuals don’t necessarily carry a bigger handicap. Consequently, there is not necessarily a correlation between signaler quality and the “handicap” nor is there necessarily a correlation between signal size and signal cost, across signalers of different quality.

differentials forming the basis of signalling are heritable? The object of the present paper is to provide, again employing the technique of exact instantiation, a demonstration that the Truthful Signalling Hypothesis (TSH) does indeed – within certain parameter ranges – extend to the case of heritable quality.

Here is the paradox of signalling equilibrium models as applied to mating choices. If females are attending to truthful signals, then higher-quality (hence higher-signalling) male contenders must necessarily win disproportionate mating success. So, assuming quality is heritable, in the next generation the high-quality high-signalling males will increase in representation in the population. This process, continuing over the generations, would seem to force the low-quality males to extinction. (Except possibly for minimal representation due to mutation pressure.) But if signalling is to persist, both low-quality and high-quality males must remain substantially present in the population. This seeming contradiction was what led R.A. Fisher (1958 [1929], p. 152) to postulate a runaway disequilibrium process instead. Another alternative, the so-called "Hamilton-Zuk hypothesis" (Hamilton and Zuk 1982), intended as a biologically plausible solution to the paradox of lost genetic variation, is that parasite-host coevolutionary cycles may result in a never-ending chase after changing optima.

Our resolution of the paradox involves an economic-evolutionary principle – we call it the Malthusian Equi-Marginal Principle. To wit, that under selection pressures the relative numbers of higher and lower-quality organisms will change until, in equilibrium, not the average but the marginal levels of quality will be equalized. Each type signals until the marginal value of more signaling is zero. That results in both types growing until density-dependent competition within types results in reproductive success where the proportions of both types stabilize. Since the marginal value of signalling falls with increasing numbers for each type regardless of the quality of that type, in equilibrium the marginal values of signalling are equal for both types despite the fact that the reproductive success is larger for higher quality than for lower quality organisms. (This will be spelled out in detail later on.) The analogous economic equilibrium condition is that, in a competitive industry, no entering marginal firm can do better than earn zero profit, while no exiting firm can do any better inside than outside the industry.

The present discussion follows the procedural sequence of our preceding article that dealt with the non-heritable case. We set forth an explicit general equilibrium system of equations, an analytic system that weaves together optimization conditions on the individual choice level together with the balancing conditions on the global level needed to make all the individual decisions consistent with one

another. This system of equations is then solved, showing that – subject to certain parametric limitations – heritable quality differentials are indeed consistent with the Truthful Signalling Hypothesis.

The measure of quality used here, fitness or reproductive success (RS), is defined in terms of female offspring only. A male's quality is the number of viable daughters that, if chosen as a mate, he can father and possibly help rear into the next generation. (Of course the mother's quality is also involved, but in this analysis all females are assumed identical.) Male quality consists of a heritable endowment, which we call endowed quality, which is in part dissipated to the extent that the male expends resources generating signals. However, the individual male dissipates some of his endowment in order to generate signals. So endowed quality is only potential fitness. The male's net quality, which is the trait of interest to females, is what remains after deducting the male's incurred signalling cost. More energy devoted to signalling, for example, may mean less available for paternal care.

The analysis that follows employs a number of other simplifying assumptions, among them: (a) An infinitely large population. (b) Only two male types, high quality (H) and low quality (L), constituting respective fractions π and $1-\pi$ of the population -- fractions that will be changing under evolutionary pressures. (c) Within each quality type, all males are identical. (d) Also, all females (F) are identical. (e) The H and L male types summed together equal the females in number.

The various agents are assumed to optimize, that is, each individual is viewed as maximizing reproductive success subject to the relevant constraints. (No actual mental processing need be involved in such "as if" optimization. Evolutionary selection dictates that the surviving organisms and strategies are those that succeed in maximizing RS, no matter how such optimal solutions are arrived at.) An equilibrium is defined by the property that no individual, male or female, can profitably deviate. In biological terminology, we are eschewing group-selection arguments. So the equilibrium is characterized by mutual consistency among all the individual males' decisions to emit signals and all the individual females' choices as to allocating mating capacity in response to those signals.

The analytic procedure is to tentatively assume that the Truthful Signalling Hypothesis is valid. Then the high-endowed-quality and low-endowed-quality types H,L are also respectively the bigger-signal and smaller-signal types (indexed as 1,2). Signalling types 1 and 2 will therefore be represented in the same population proportions $\pi, 1-\pi$ as the H and L quality types. In accordance with the TSH, the model must also incorporate the fact that females "believe" the signals. Thus, letting m and $1-m$ denote the proportions of the typical female's mating capacity devoted to the big-signal and small-signal types respectively, it must be that in equilibrium $m > \pi$. If a complete and consistent set of equations can be found that generates such an equilibrium, while allowing π to vary in response to the

male types' relative degrees of reproductive success, we regard the internal logical consistency of the Truthful Signalling Hypothesis as validated even under conditions of heritable quality.

Once a solution is found for the equation system, it remains necessary to test for evolutionary stability. For a particular solution to be valid, an arbitrary displacement must generate evolutionary forces – in this case, changes in relative population numbers of the H and L males – tending to restore the system toward, rather than force it away from, the candidate equilibrium.

Section 2 that follows sets forth and explains the model, showing how it generates equilibria consistent with the Truthful Signalling Hypothesis. Section 3 provides a baseline numerical solution. Section 4 discusses system breakdown, and the conditions of its occurrence. Section 5 discusses simulations for the existence of equilibrium, considering paired-parameter variations. Section 6 extends to single-parameter variations. Section 7 concludes.

2. The signalling model with heritable quality – evolutionary equilibrium

In this section the elements of the male choice situation are first summarized, followed by a similar consideration of female choices. After that the male and female optimization conditions are outlined. Next we turn to the crucial Malthusian Equi-Marginal Principle, which resolves the paradox described above – that the high-quality high-signalling males are always doing better (earning higher reproductive sense) than their low-quality low-signalling rivals, yet need not force the latter to extinction. A congestion effect prevents mating exclusively with high-quality males, and we will see that an equilibrium is possible where both types enjoy non-negative but different reproductive success, though equal marginal values. In each case, we emphasize, what is provided is not an abstract general proposition but an exact instantiation with functional forms, with an explicit solution consistent with the Truthful Signalling Hypothesis under conditions of heritable quality.

The modelling aim is to create a complete and consistent set of equations that generates the two crucial features of the TSH: (1) That the male signals are “truthful”. The condition is $s_H \equiv s_1 > s_L \equiv s_2$, where high and low quality are symbolized by the subscripts H and L, and big versus small signals by the subscripts 1 and 2. (2) That the signals are “believed” by the females. This means that the females devote a more-than-proportionate fraction m of their mating capacity to the high-quality high-signalling males. (Yet, since the L-type males do not to extinct, the fraction remains short of unity: $\pi < m < 1$.)

2.1 Male choices – the elements

The high-quality and low-quality male types (indexed as H,L) are respectively, by hypothesis, also those emitting bigger and smaller signals (indexed as 1,2). Each male's endowed quality e_i ($i = 1,2$) – his available resources, external or internal -- can be employed either to generate signals of magnitude s_i or else to generate net quality n_i as a mate. We write this as a conventional linear cost trade-off, i.e. $n_i = e_i - b_i s_i$ for $i = 1,2$ Male Endowment Constraint (1)

The b_i are conversion coefficients (assumed constant) between male resources and levels of signalling, i.e., they represent the per-unit or marginal costs of signalling -- in general differing as between the two male types. Since the coefficient of n_i is unity, endowed quality e_i and net quality n_i are denominated in the same “currency”. And since offspring (where we count only daughters, there being an equal number of sons) are of equivalent quality, only numbers matter. So for each male type, n_i can be interpreted simply as the number of daughters per mating that survive into the next generation.

Let m be the proportion of a typical female's mating capacity going to the high-quality (H) male type, the remainder of course going to the low-quality (L) type. When the Truthful Signalling Hypothesis is valid, these will also be the proportions going respectively to the big-signallers and small-signallers. And since $\pi, 1-\pi$ are the population proportions of the two types, the H and L per-capita mating success rates will be m/π and $(1-m)/(1-\pi)$ respectively.

As a third essential condition of a valid equilibrium solution consistent with the Truthful Signalling Hypothesis, it must be the case that not only is $e_1 > e_2$ but also $n_1 > n_2$. In other words, the H-type males not only have initially higher endowed quality; their net quality must also remain higher even after expending more resources upon signalling than the L-type males.

A male of either type will choose (that is, will be selected “as if” he were choosing) the signalling level that maximizes his fitness or reproductive success RS_i – which is the product of his per-capita mating success, his net quality n_i , and the female's mating capacity K (to be described below):

$$RS_1 = K \left(\frac{m}{\pi} \right) n_1 \quad \text{and} \quad RS_2 = K \left(\frac{1-m}{1-\pi} \right) n_2 \quad \text{Male Reproductive Success (2)}$$

If the females “believe” the signal, then $m/\pi > 1$. So the H males will have more than one mating per capita, and the L males less than one. The RS measures cannot be negative. First, K, m, π are between zero and one. Second, if e_i in (1) is very small, the male of type i will adjust his signalling downwards,

if necessary to $s_i = 0$ which gives $e_i = n_i$. Consequently, RS_1 and RS_2 are positive or equal to zero.

2.2 Female choices – the elements

With the aim of maximizing her reproductive success, each female will be choosing the fractions m and $1-m$ of her mating capacity going respectively to the high-signalling and low-signalling males. However, to prevent her from devoting 100% of her mating capacity to the bigger-signalling males (since she “believes” them to be also the male type of higher net quality), some kind of diminishing returns must be operative. The model here postulates a form of congestion or search costs for choosiness. Females may have to wait in line for the preferred males, or spend time and effort searching for them. The consequence is that, in attempting to mate disproportionately with such males, i.e., to raise her chosen m above π , a female must accept some reduction of her mating capacity K .

A specific instantiation is:

$$K = 1 - h(m - \pi)^2 \quad \text{Female Mating Capacity (3)}$$

The “congestion coefficient” h , another of the fixed parameters of the model, scales the extent to which attempting to make m exceed π impacts negatively upon female mating capacity. Somewhat akin to congestion would be dilution of paternal care on the part of preferred males.

Let M denote the average quality of the typical female’s mates, weighted by the mating fractions m and $1-m$:

$$M \equiv mn_1 + (1 - m)n_2 \quad \text{Average Net Quality of Female’s Mates (4)}$$

Then the female’s payoff, her reproductive success in terms of number of daughters surviving into the next generation, is:

$$RS_F = KM = \pi RS_1 + (1 - \pi)RS_2 \quad \text{Female Reproductive Success (5)}$$

Female per-capita reproductive success equals mating capacity times the weighted average of the two male qualities. Our equations (2) and (5) make our instantiation a multiplicative signalling model. See Getty (1998ab,2002) for a discussion of the distinction between additive and multiplicative models within the context of Grafen’s (1990ab) model and other models.

2.3 Optimization and equilibrium

The female will be selected to maximize her individual reproductive success by choosing the fraction of her mating capacity to devote to the high-signalling males. In this model all females are identical, and each individual female’s chosen mating fraction is independent of the choices of other

females, though the mating fraction m depends on the congestion or search costs for choosiness experienced individually by each individual female as expressed by K in equation (3) which plays a role in her reproductive success. So the “typical” or representative female optimizes by differentiating RS_f with respect to m , leading to the first-order condition:

$$K(n_1 - n_2) = -DM \quad \text{Female F.O.C. (6)}$$

where $D \equiv dK/dm$ is the marginal congestion effect:

$$D = -2h(m - \pi) \quad \text{Marginal Congestion Effect (7)}$$

The representative female balances the marginal cost against the marginal benefit of shifting a unit of her mating capacity from the smaller-signalling type-2 males to the bigger-signalling type-1 males. The marginal benefit of shifting, the left-hand side of (6), is the difference in net qualities $n_1 - n_2$ weighted by her mating capacity K . The marginal cost, the right-hand side, is the loss of mating capacity due to congestion, multiplied by the average net quality of the males she would otherwise have mated with. (It is straightforward to verify that the second-order condition for a maximum is satisfied.)

Following a novel concept introduced in our earlier paper, a Mating Success Function (MSF) is employed to express female sensitivity to male signalling differentials. If type-H and type-L males are signalling at the respective levels s_1 and s_2 , the MSF tells us how the signals translate into mating success. Put another way, the MSF specifies the degree to which the representative female attends to the signals in choosing her mating fractions m and $1-m$. Instantiating with a specific functional form, we postulate that females will respond to the male signals in accordance with:

$$\frac{m}{\pi} = \frac{1-m}{1-\pi} \left(\frac{s_1}{s_2} \right)^r \quad \text{Mating Success Function (8)}$$

Thus, the ratio in which a female distributes her mating capacity between the high-signalling and the low-signalling male types reflects their proportionate representation in the population (the first factor on the RHS of (8)) augmented by a signalling factor – the ratio of the signalling efforts raised to a power $r > 0$. Here r , which scales the extent to which differing signalling intensities translate into mating success, is the “signalling decisiveness parameter”. If $r = 0$ there is no effect at all: the females pay no attention to signals and mate at random, so that $m = \pi$. The higher is r the more decisive are the signals in bringing about mating success. The MSF is an analog of what has been called the Contest Success Function in economic conflict theory (Tullock 1967, Hirshleifer 1989, 1991,

Skaperdas 1996, and see also Grafen 1990b, p. 522).

Although r is parametric from the point of view of each and every male and female acting singly, for the analytic system as a whole the magnitude of r is an endogenous variable. More specifically, r is the equilibrating variable that glues together the male and female decisions. It reflects the overall “market conditions” in the signalling process – the willingness of the different types of males to emit signals, and of the females to attend to them.

Given the females’ choice of the mating fraction m , on the male side there will be in equilibrium a chosen pair of signalling levels s_1 and s_2 for the H and L types respectively. Given that, within each type, all males are identical, each individual male’s chosen signalling level is independent of the choices of the other males of his type. So for each male type we can think of a typical or representative individual as optimizing by differentiating RS_1 or RS_2 , as the case may be, with respect to the respective signalling levels s_1 or s_2 -- leading to the first-order conditions:

$$b_1 s_1 = r(e_1 - b_1 s_1) \quad \text{and} \quad b_2 s_2 = r(e_2 - b_2 s_2) \quad \text{Male F.O.C.'s (9)}$$

So, apart from the fixed parameters, the equilibrium male signalling levels respond only to the intermediating “decisiveness” parameter r that signifies the extent to which the females attend to the signals. Furthermore, s_1 is independent of s_2 and N_2 , except through r .

Eliminating r from (9) leads to the important result:²

$$s_1 > s_2 \Leftrightarrow b_1 / e_1 < b_2 / e_2 \quad \text{Truthful Signalling Condition (10)}$$

This crucial proposition is the exact relationship between endowment levels and unit signalling costs required, in this formulation, for the TSH to hold. As the simulations will confirm, the Truthful Signalling Hypothesis can be valid even if the H-type males have higher unit signalling costs than the L-type males ($b_1/b_2 > 1$) – provided this disadvantage is sufficiently counterbalanced by the H-type males’ superiority in endowed quality (e_1/e_2 is sufficiently large).

2.4 Malthusian Considerations and Evolutionary Equilibrium

This section turns to the conditions for evolutionary equilibrium when quality is heritable. To recall the paradox, if females are attending to truthful signals, then higher-quality (hence higher-signalling) male contenders must necessarily win disproportionate mating success. So in the next

² This can be interpreted as a “decreasing-proportional-marginal-cost” criterion for truthful signaling, which appears to have been independently discovered by Eshel et al. (2002), Hausken and Hirshleifer (2004), Houston (2003), Proulx et al. (2002). We thank Getty (2005) for pointing this out to us.

generation the high-quality high-signalling males will increase in representation in the population. Thus π would steadily rise. This process, continuing over the generations would seem to imply inevitable extinction of the low-quality males. But if signalling is to persist, both low-quality and high-quality males must remain substantially present in the population. We believe that this offers a potentially more general solution than Hamilton and Zuk's (1982) popular solution that parasite-host coevolution solves the paradox.

Allowing for diminishing returns, so that as π rises RS_1 falls relative to RS_2 , does not itself suffice to resolve the paradox. So long as any positive difference between RS_1 and RS_2 persists, π will remain subject to upward pressure. But $RS_1 = RS_2$ is not a possible equilibrium condition. In (2), if m exceeds π then necessarily n_1 must be less than n_2 . But as a condition of equilibrium, the H-type males must remain of higher net quality ($n_1 > n_2$) despite expending more resources in signalling.

As suggested above, the escape from this paradox rests upon realizing that the true criterion, for balancing the relative numbers of high-quality versus low-quality males, consists of equating not average fitness (RS_1 or RS_2) but marginal fitness – the Malthusian Equi-Marginal Principle.

The Malthusian Equi-Marginal Principle is the essential feature permitting an evolutionary equilibrium with heritable quality that also meets the essential conditions of the Truthful Signalling Hypothesis: to wit, $s_H \equiv s_1 > s_L \equiv s_2$, and $\pi < m < 1$. The upshot is that, although the H-type males are always doing better on average ($RS_1 > RS_2$), and consequently are gaining a disproportionate fraction of the female mating capacity ($m > \pi$), there is a limit to how much they can increase in numbers relative to the low-quality males. Once the marginal fitness MRS_1 of an H-type male is no higher than the marginal fitness MRS_2 of an L-type male, the numbers of the two types stabilize.

Returning to the equation system, the total female population N , also considered as a variable, is by assumption equal to the sum of the two male types:

$$N = N_1 + N_2 \tag{11}$$

Changes in the fractions π , $1-\pi$ of the two male types will affect the degrees to which each is pressing upon the environments. As π grows, the H-type is likely to run into a kind of Malthusian diminishing returns, tending to reduce its endowed quality e_1 . Correspondingly, of course, the reduced environmental pressure is likely to increase e_2 , the endowed quality of the L-type males. We instantiate the relation between endowed qualities and the respective population sizes with the following specific functional form:

$$\begin{aligned} e_1 &= E_1 \exp\{-q_1 N_1\}, \\ e_2 &= E_2 \exp\{-q_2 N_2\} \end{aligned} \quad \text{Malthusian Diminishing Returns (12)}$$

The constants E_1 and E_2 are the underlying quality parameters. The endowed qualities e_1 and e_2 , previously interpreted as constants, now become variables responding to population size. The constants q_1 and q_2 are “the Malthusian crowding parameters”. They are measures of diminishing returns. As these parameters rise in numerical value, for each male type endowed quality falls off more rapidly as its numbers increase. Equation (12) introduces the important idea of resource competition. For simplicity we assume that it is strictly within types, implying that there is no resource competition across the high and low quality types. That is, the model focuses on signalling competition, and the important characteristic of (12) is that the endowed qualities e_1 and e_2 both fall off as population sizes N_1 and N_2 increase. If N_i approaches infinity, which causes N to approach infinity, e_i approaches zero, which according to (2) causes the reproductive success RS_i to approach zero, $I=H,L$. If both N_1 and N_2 approach infinity, RS_F approaches zero according to (5). Equation (12) implicitly accounts for both births and death, so if N_i increases, there must be more births than deaths. In a steady state equilibrium, all variables level out, and we get $\partial N_i / \partial t = 0$ for $N_i > 0$, and similarly for all the other variables, where t is time.

Following the usual derivation provided in economic textbooks for the algebraic relation between average and marginal magnitudes, the Marginal Reproductive Success for the two male types can be determined. Let us define the "total" RS measures for the two male types as groups, as $TRS_i = N_i RS_i$. The "marginal" measures, as new members of the respective populations enter, are defined as in standard economic texts, by differentiating with respect to the population sizes. This gives $MRS_i = \partial(TRS_i) / \partial N_i = RS_i + N_i \partial RS_i / \partial N_i$. Since $\partial RS_i / \partial N_i$ is negative, as expected the "marginal" RS measures will be smaller than the "average" measures. Inserting (1) into (2) for the high quality males gives $RS_1 = K(m/\pi)(e_1 - b_1 s_1)$. When differentiating RS_1 w.r.t. N_1 we take K and (m/π) as given (which means that they are interpreted as constants in the derivation) since these are determined in the "female module". And we take s_1 as given since it is determined in the "male module". This gives $\partial RS_1 / \partial N_1 = K(m/\pi) \partial e_1 / \partial N_1$, where $\partial s_1 / \partial N_1 = 0$. The reason for this different treatment of e_1 and s_1 is that the endowed quality e_1 is a variable responding directly to

population size N_i as specified in (12). In contrast, the signal s_i is determined in the "male module" by derivating RS_i w.r.t. s_i taking K , r , and e_i as given, which means that the population size N_i is also taken as given. Hence although s_i in (9) can be expressed in terms of e_i which depends on N_i , s_i is determined taking N_i as given. Each male thus chooses his signal taking population sizes as given when optimizing. This does not mean that signalling is independent of population sizes, but the dependence is indirect through the other variables such as the mating fraction m , the glue variable r , and the other variables. In an equation system, of course, all variables depend on all other variables unless we deal with two or several independent equation systems. Using (12) and applying analogous reasoning for the L-type males gives

$$\begin{aligned} MRS_1 &\equiv RS_1 + N_1 \partial RS_1 / \partial N_1 = RS_1 (1 - q_1 E_1 N_1 \exp\{-q_1 N_1\} / n_1) \\ MRS_2 &\equiv RS_2 + N_2 \partial RS_2 / \partial N_2 = RS_2 (1 - q_2 E_2 N_2 \exp\{-q_2 N_2\} / n_2) \end{aligned} \quad \text{Definitions of } MRS_i \quad (13)$$

The population fraction represented by the H-type males, π , is:

$$\pi = \frac{N_1}{N_1 + N_2} \quad \text{Definition of } \pi \quad (14)$$

Finally, the Malthusian Equi-Marginal Principle dictates that, in evolutionary equilibrium:

$$MRS_1 = 1 = MRS_2 \quad \text{Conditions of Evolutionary Equilibrium} \quad (15)$$

Equation (15) stands in contrast to the common stability criterion that $RS_1 = RS_2$. However, in nature, and in our model as well, stability over time occurs exactly when $RS_1 > RS_2 \geq 0$. We showed in section 2.1 that the RS measures cannot be negative. The high-quality males achieve higher reproductive success RS_1 than RS_2 for the low-quality males. Because of congestion or search costs for choosiness, females will not mate exclusively with high-quality males, regardless how large is RS_1 , as long as RS_2 is marginally positive. This means that neither the mating fraction m , nor the fraction π of high-quality males, can increase to one, though we have $m > \pi$ since females to a limited extent (constrained by congestion or search costs for choosiness) prefer high-quality males over low-quality males. In this light, equating RS_i and RS_j does not make sense. High-quality and low-quality males cannot earn equal reproductive success. Instead, each male maximizes his own reproductive success and signals until the marginal value of more signaling is zero, which gives an equilibrium

where both male populations stabilize, which also stabilizes the female population. In doing so each male takes his own endowment, other characteristics, the female mating fraction, and congestion or search costs for choosiness as experienced by females, into account. There is no comparison of reproductive success across the male types. A high-quality male cannot switch to become a low-quality male, and a low-quality male cannot switch to become a high-quality male. Consistent with economic reasoning, equilibrium numbers are determined by the marginal conditions. The equilibrium is determined by the marginal profitability of male entry of the two types, determined by birth and death processes where the relative proportions of the two male types are determined by female choice. As the population size increases for each type, the marginal value of signalling decreases, regardless of the quality of that type. Hence in equilibrium the marginal values of signalling are equal for both types despite reproductive success being larger for high-quality males than for low-quality males.

Inserting (15) into (13) and requiring $RS_1 > RS_2$ implies that we cannot have $N_1 = 0$ and $N_2 > 0$. If we hypothetically assume $N_1 > 0$ and $N_2 = 0$, it follows from (14) that $\pi = 1$, and from $m > \pi$, that $m = 1$. When $m = \pi$, we get $K = 1$, $RS_1 = n_1 = RS_2 = n_2 = 1$, $b_1 s_1 = r = b_2 s_2$, $E_1 = 1 + b_1 s_1 = 1 + r$, $E_2 = 1 + b_2 s_2 = 1 + r$, which is a contradiction since we require $E_1 > E_2$. Consequently, in the evolutionary equilibrium we must have $N_1 > 0$ and $N_2 > 0$ so that none of the two male populations go extinct.

Taking stock at this point, the equation system has 20 variables: $m, s_1, s_2, n_1, n_2, K, M, r, D, e_1, e_2, N, N_1, N_2, RS_1, RS_2, RS_F, MRS_1, MRS_2$, and π . Counting equations, (1),(2),(9),(12),(13),(15) provide two each and (3)-(8) plus (11),(14) provide one each. (That the numbers of equations and variables match up does not of itself demonstrate that the system is internally consistent and complete, but the numerical simulations that follow will verify the formal validity of the equation system.)

For the simpler case of non-heritable quality dealt with in our earlier paper, it was possible to find an explicit analytic solution for the equation system as a function of the underlying exogenous parameters. Owing to the increased analytic complexity, this has not proved possible for the case of heritable quality. But our numerical baseline solution will suffice to demonstrate, by direct example, the logical completeness and consistency of the equation system. After exploring a number of the features of the baseline solution, we will examine how the solution changes in response to exogenous variations of a number of the important determining parameters.

3. A baseline solution

In Table 1 the columns to the left show the parameter settings for the baseline solution, while the

columns to the right define the variables and display the numerical solution values.

[Table 1 about here]

3.1 Features of the baseline solution

At the chosen baseline parameter values, the Truthful Signalling Hypothesis is validated.

1. The H-type males, characterized by higher underlying quality ($E_1 = 10 > E_2 = 5$) and endowed quality ($e_1 = 5.699 > e_2 = 3.549$) do indeed signal more heavily than the L-type males ($s_1 = 3.527 > s_2 = 1.098$). Despite this heavier signalling burden, the signalling remains “truthful” (that is, the high signalling males remain of superior quality) in terms of net quality after taking signalling costs into account: $n_1 = 3.936 > n_2 = 2.451$.
2. The females “believe” the signals, that is, they grant the higher-quality males a disproportionate share of the matings ($m = 0.409 > \pi = 0.291$).
3. Since π remains well below unity, the high-quality males fall well short of forcing the low-quality males to extinction.
4. The inferior-quality males remain in the population, even though their average reproductive success RS_2 is far lower than the RS_1 of the H-type males ($1.986 < 5.380$), because, at equilibrium, the marginal measures of reproductive success for both types equal unity (the Malthusian Equi-Marginal Principle).

3.2 Evolutionary stability of the baseline solution

An acceptable solution must not only satisfy the system of equations but must also be evolutionarily stable. The test is, if the number N_i of either type of male is arbitrarily displaced from the candidate equilibrium value, do Malthusian forces tend to restore the equilibrium – or do they lead to further divergences from it? Thus, for evolutionary stability, $d(MRS_1/dN_1)$ and $d(MRS_2/dN_1)$ must both be negative as either N_1 or N_2 is displaced away from its equilibrium value. Differentiating and applying $dRS_1/dN_1 = dRS_1/de_1$ leads to:

$$\frac{dMRS_1}{dN_1} \equiv \frac{RS_1(q_1 N_1 - 2)q_1 E_1 \exp\{-q_1 N_1\}}{n_1} < 0 \text{ when } q_1 N_1 < 2 \quad \text{Evolutionary stability (16)}$$

And similarly for displacements of N_2 .

(Owing to the complexity of the equation system, we have not been able to reduce the stability conditions to direct functions of the exogenous parameters. So stability cannot be determined by analytic inspection, but has to be tested by simulation.)

In Figure 1a the solution values for MRS_I do indeed display negative slope as N_I increases or decreases away from its equilibrium value. (The plotted values are found by disabling the equation $MRS_I = 1$ and then solving the reduced system for the values of MRS_I implied by values of N_I in the neighborhood of the solution value.) Similarly, Figure 1b shows that the curve for MRS_2 also has negative slope in the neighborhood of the equilibrium value of N_2 . This verifies that the baseline solution not only satisfies the system of equations but is also evolutionarily stable.

[Figure 1 about here]

4. System breakdown

System breakdown (SB) occurs when no solution exists. In Figure 2, with N_I on the horizontal axis, the relevant condition of equilibrium is $MRS_I = 1$. (An analogous diagram could be constructed for N_2 , using the condition $MRS_2 = 1$.) If the equation $MRS_I = 1$ is disabled and the remainder of the system solved for MRS_I , for any given set of parameters a curve like those pictured is generated. Varying one of the parameters (in this case, b_1) while holding all the other parameters at their baseline values, the rightmost curve for $b_1=1.312$ shows that a solution exists – since the generated MRS_I curve intersects the line $MRS_I = 1$. But the leftmost curve for $b_1=1.315$ never intersects $MRS_I = 1$, so no solution exists for this larger value of b_1 . The middle curve gives the maximum value $b_1=1.3135$ where a solution exists. This b_1 value is far above the baseline $b_1=0.5$, and the population size of H-type males decreases to $N_I=0.5808$. H males suffer because of the high unit cost of signalling. A higher cost cannot be sustained while keeping the Marginal Reproductive Success as low as $MRS_I = 1$.

[Figure 2 about here]

5. Simulation tests for existence of equilibrium – paired-parameter variations

By jointly varying related pairs of parameters, this section explores the question of system breakdown (SB) -- or, equivalently, the existence of equilibrium in our equation system. In Figure 3a the shaded stable region (SR) to the right and below the straight solid linearly increasing line represents the set of q_1, q_2 pairs – the Malthusian crowding parameters from equation (12) – that lead to (evolutionarily stable) solutions of the equation system. These parameters measure the respective intensities of diminishing returns, that is, for each male type how rapidly quality falls off as its

population numbers increase.

[Figure 3 about here]

Inserting (1),(2),(8),(12),(14) into (15), and applying from (1) and (9) that $b_i s_i = r n_i$ gives

$$\frac{n_1(1 - N_1 q_1(1 + r))}{n_2(1 - N_2 q_2(1 + r))} = \left(\frac{s_2}{s_1} \right)^r \quad (17)$$

For the numerator and denominator on the LHS to be positive we must have $r < (1 - N_1 q_1)/(N_1 q_1)$ and $r < (1 - N_2 q_2)/(N_2 q_2)$. Requiring $n_1 > n_2$ and $s_1 > s_2$, (17) implies

$$\{n_1 > n_2 \text{ and } s_1 > s_2\} \Rightarrow \frac{N_1 q_1}{N_2 q_2} > 1 \Rightarrow \frac{b_1}{b_2} < \frac{e_1}{e_2} = \frac{b_1 s_1}{b_2 s_2} = \frac{n_1}{n_2} < \frac{E_1}{E_2} \quad (18)$$

where the second implication follows from using (1),(9),(10),(12). At the end of section 2 we proved that we must have $N_1 > 0$ and $N_2 > 0$ in the evolutionary equilibrium. Equation (18) specifies for finite values of N_1 and N_2 that q_1 cannot be too small relative to q_2 . For each value of q_2 , Figure 3a shows the lowest value of q_1 that gives a stable region. Intuitively, for a solution to exist, diminishing returns must operate with greater intensity upon the superior-quality population, else it would eventually drive the lower-quality population to extinction. Hence $N_1 q_1$ cannot be too small

Figure 3b is a corresponding diagram for the parameter-pair b_1, b_2 – the respective marginal costs of signalling. There has been some discussion in the literature whether, consistent with the idea that signalling must reflect a handicap, for a TSH equilibrium it must be that $b_1 > b_2$. See Grafen (1990b:522), Godfray (1991:329), Hurd (1995:219), Szamado (1999), Getty (1998ab,2002), Nur and Hasson (1984). Eshel et al. (2002) show that decreasing marginal costs are unnecessary, while decreasing proportional marginal costs are necessary. Our earlier paper showed that, assuming non-heritable quality, this was not a strictly necessary condition, although for an interior equilibrium to exist it must be the case that b_1 cannot exceed b_2 by too wide a margin. Figure 3b reveals that essentially the same result applies also when quality is heritable. The entire shaded region above the 45° line is part of the solution region, together with a shaded sector below that indicates the extent to which solutions are possible even when $b_1 > b_2$. – that is, when the H-type males must incur heavier per-unit signalling costs

It might be wondered how it is that solutions exist even when b_1 and b_2 rise without limit. The

reason, as can be seen in equations (9), is that the signalling levels s_1 and s_2 are simultaneously falling off toward zero. Indeed, as we will see in the single-parameter simulations below that show more detail, as the levels of per-unit signalling costs b_1 and b_2 rise, the corresponding total signalling costs $b_1 s_1$ and $b_2 s_2$ actually fall.

6. Simulation tests – equilibrium implications of single-parameter variations

In order to explore some of the conditions bearing upon the existence of solutions validating the Truthful Signalling Hypothesis, the preceding section studied joint variations of the parameter-pairs q_1, q_2 and b_1, b_2 . In order to generate more detailed implications for the dependent variables – among them the signalling levels s_1 and s_2 , the population sizes N_1 and N_2 , the degrees of reproductive success RS_1 and RS_2 , and the value of the signalling decisiveness parameter r – this section explores variations in a number of the crucial parameters taken one at a time.

6.1 Parametric variation of relative underlying quality – E_1 vs. E_2

Figure 4 shows how equilibrium values of several of the crucial variables respond to parametric variations of E_1 – the underlying quality of the H-type males – relative to a fixed $E_2 = 5$. The underlying quality of the H-type males is allowed to vary both upward and downward from its baseline value $E_1 = 10$ (shown in bold), all the other parameters being held at their baseline values.

[Figure 4 about here]

In the top panel of Figure 4 we see that as the H-type males rise in quality, as expected both m and π – their fractional mating success and their representation in the population – increase. In the lower panel especially s_1 – the signalling level of the H-type males – increases dramatically in E_1 . The L-type males follow suit to their best ability with s_2 , which is costly, and s_2 increases concavely. At the same time the population size N_2 falls rapidly. (Division with 2 for the population sizes N_1 and N_2 is for scaling convenience.) As E_1 increases above $E_2=5$, the decisiveness r first increases with strong concavity. The H-type males seek to separate or distinguish themselves from the L-type males through increased signalling, which gives increased decisiveness. This is costly when E_1 is only marginally larger than E_2 , so the population size N_1 of H-type males first falls slightly, and thereafter increases slightly, i.e. is U formed. The decisiveness r is inverse U formed, reaches a maximum for $E_1=15.35$, and thereafter decreases very slightly. As expected, the reproductive success RS_1 of H-type males increases in E_1 , while RS_2 decreases, while female reproductive success RS_F is intermediate and increases moderately. Also the net quality n_1

increases strongly, while n_2 is slightly U formed. Finally, for the lowest underlying quality for the H-type males, $E_1=E_2=5$, signalling ceases, $s_1=s_2=0$, which also causes zero signalling decisiveness $r=0$.

6.2 Parametric variation of relative underlying quality – b_1 vs. b_2

Figure 5 shows response to parametric variations of b_1 – the unit signalling cost of the H-type males – relative to a fixed $b_2 = 5$.

[Figure 5 about here]

The most intuitive result is that the reproductive success RS_1 of H-type males shows the largest decrease in b_1 . Also intuitive is that the signalling of H-type males decreases convexly from infinity at zero cost $b_1=0$. When b_1 is below b_2 , L-type males realize their signalling inferiority, and s_2 is very low, which also causes decisiveness r to be low. L-type males' underlying quality is half that of H-type males', $E_2=E_1/2$, and the low signalling allows for sustaining a large population N_2 of L-type males. L-type males have a reproductive success RS_2 around 1/3 that of H-type males. However, as b_1 increases toward b_2 , male competition becomes more fierce and decisive. L-type males realize a benefit from signalling, and s_2 increases. This causes the population N_2 of L-type males to fall off dramatically, which is remarkable. That is, higher unit cost for H-type males causes higher decisiveness and a lower population N_2 . The population size N_1 of H-type males falls off too, but less dramatically.

As b_1 increases above $b_2=0.5$, a new effect starts to operate. To wit, N_2 falls off more than N_1 , and s_2 increases. Consequently, H-type males cannot allow s_1 to decrease too much, so s_1 levels out, and eventually increases, despite the increased unit cost b_1 of such signalling! s_1 is thus U formed. Although s_1 increases, s_2 increases more and convexly since L-type males has the same fixed unit cost of signalling. r also increases convexly. This development naturally gives system breakdown at some upper value of b_1 , specified as $b_1=1.3135$ in Figure 5, which also can be seen from Figures 2 and 3b. At this breakdown the population sizes N_1 and N_2 is pushed very close to zero, though they cannot be pushed all the way to $N_1=N_2=0$ as shown in section 5. The increased signalling s_2 , as b_1 increases, causes also the reproductive success RS_2 of L-type males to decrease, though less than RS_1 decreases. RS_F , n_1 , and n_2 decrease too. Finally, the fractional mating success m , and representation π in the population, of H-type males, are almost constant but increase slightly. Two opposite effects operate here. On the one hand, increasing b_1 is a disadvantage for H-type males which should decrease m and π . On the other hand, the rapidly decreasing N_2 and eventual increase of s_1 sustain female interest in H-type males causing slight increase in m and π .

7. Conclusion

The Handicap Principle (Zahavi 1975) has gained increased acceptance. Grafen (1990a,b) presented a formalization of the principle, and by direct instantiation its internal logical consistency has recently been demonstrated by Hausken and Hirshleifer (2004). These analyses have assumed non-heritable quality. The main concern of biologists is however with heritable quality. Assuming heritable quality leads however to a seeming paradox. On the one hand high-quality high-signalling males will increase in representation in the population through the generations. On the other hand, for signalling to persist both low-quality and high-quality males must remain present. Fisher (1929) suggested resolving the paradox with a runaway disequilibrium process, and Hamilton and Zuk (1982) proposed that parasite-host coevolutionary cycles may cause never-ending chases after changing optima. This article takes a quite novel approach to resolving the heritability paradox. Under selection pressures the relative numbers of higher and lower-quality organisms will change until, in equilibrium, not the average but the marginal levels of quality will be equalized. This Malthusian Equi-Marginal Principle is the key analytic innovation of the paper. In nature, and in our model as well, high-quality males achieve higher reproductive success than low-quality males in an equilibrium with stable population sizes. This is possible since females because of congestion or search costs for choosiness will not mate exclusively with high-quality males. Each male maximizes his own reproductive success and signals until the marginal value of more signaling is zero.

The equation system leading to solutions consistent with the Truthful Signalling Hypothesis contains, as key elements, a Mating Success Function which indicates how female mating choices respond to higher and lower signalling levels, and a congestion function which rules out corner solutions in which females would mate exclusively with higher-quality males. Furthermore, for evolutionary stability, the derivative of the marginal reproductive success for each male type with respect to the population size of that type must be negative. A negative derivative implies that the population size decreases for that type. This means that an out-of-equilibrium displacement to a higher population size causes lower marginal reproductive success, which reduces the population size and thus restores the equilibrium, and similarly for a displacement to a lower population size. The absolute population sizes are determined by equating the marginal reproductive success of the two male types, which gives an equilibrium with higher reproductive success for high-quality than for low-quality males.

The model developed is solvable for sets of parameters that constitute the stable region, in contrast to unstable regions where system breakdown occurs. We test the stable region and confirm

evolutionary stability. That is, an arbitrary displacement must generate evolutionary forces, in this case, changes in relative population numbers of the H and L males – tending to restore the system toward, rather than force it away from, the candidate equilibrium.

We particularly consider the unit signalling costs of the H-type and L-type males, where it has been widely believed that the former must be lower than the latter. This article confirms our earlier result that this is not necessary, though for a stable TSH equilibrium to persist the unit signalling costs of the high-quality males cannot be too much larger.

The article shows that, subject to certain parametric limitations, heritable quality differentials are consistent with the Truthful Signalling Hypothesis.

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Table 1: VARIABLE DEFINITIONS AND BASELINE SETTINGS

| Variables and baseline for Signalling Solutions | | | Settings of the Fixed Parameters | |
|---|-----------|--|----------------------------------|---|
| m | 0.408803 | Proportion of female mating capacity going to H-type males | $b_1 = 0.5$ | Signalling costs per unit for H-type males |
| s_1 | 3.526643 | Signalling level of H-type males | $b_2 = 1.0$ | Ditto for L-type males |
| s_2 | 1.097933 | Ditto for L-type males | $h = 2.0$ | Congestion effect coefficient |
| n_1 | 3.936009 | Net quality of H-type males | $q_1 = 0.4$ | Malthusian crowding parameter of H-type males |
| n_2 | 2.450758 | Ditto for L-type males | $q_2 = 0.1$ | Ditto for L-type males |
| K | 0.972132 | Female mating capacity | $E_1 = 10$ | Underlying quality of H-type males |
| M | 3.057933 | Average net quality of mated males | $E_2 = 5$ | Ditto for L-type males. |
| r | 0.447997 | Signalling decisiveness | | |
| | 4 | parameter | | |
| D | -0.472169 | Marginal congestion effect | | |
| e_1 | 5.699331 | Resource endowment of H-type males | | |
| e_2 | 3.548691 | Ditto for L-type males | | |
| N | 4.834181 | Number of females | | |
| N_1 | 1.405591 | Ditto for H-type males | | |
| N_2 | 3.428591 | Ditto for L-type males | | |
| RS_1 | 5.379719 | Reproductive Success of H-type males | | |
| RS_2 | 1.985936 | Ditto for L-type males | | |
| RS_F | 2.972715 | Ditto for females | | |
| MRS_1 | 1 | Marginal Reproductive Success of H-type males | | |
| MRS_2 | 1 | Ditto for L-type males | | |
| π | 0.290761 | Proportion of H-type males | | |

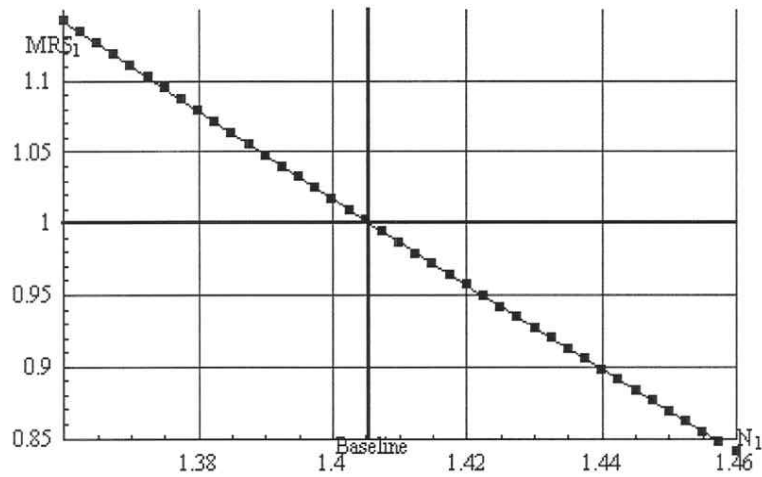


Fig. 1a. Evolutionary Stability of the Baseline Solution. MRS_1 as a function of N_1 when $MRS_1=1$ is disabled.

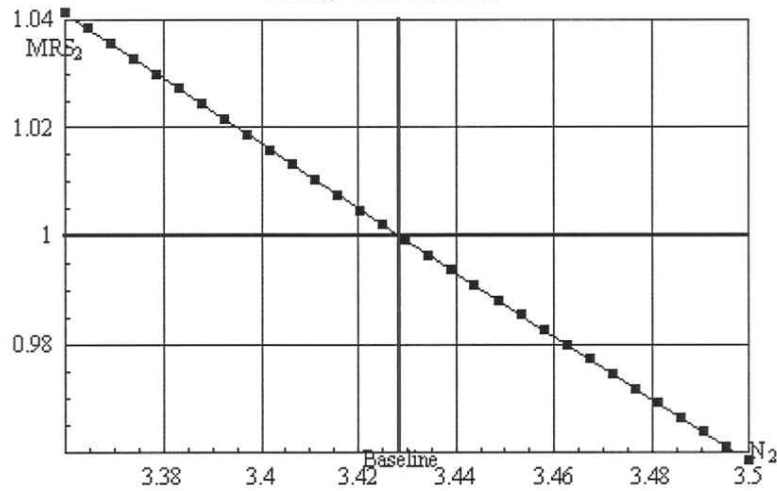


Fig. 1b. Evolutionary Stability of the Baseline Solution. MRS_2 as a function of N_2 when $MRS_2=1$ is disabled.

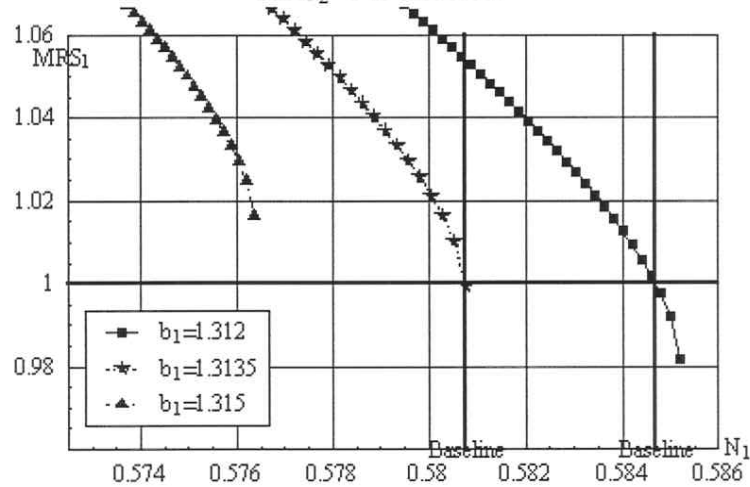


Fig. 2. MRS_1 as functions of N_1 , $MRS_1=1$ is disabled.

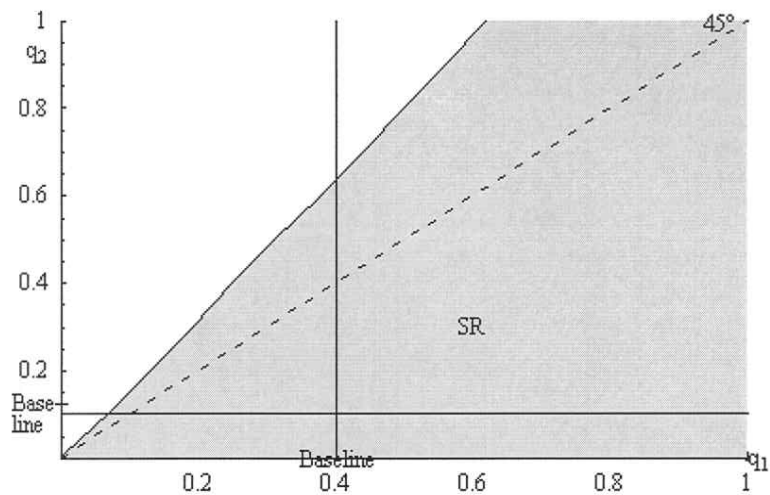


Fig. 3a. Stable region SR in a q_1 versus q_2 diagram.

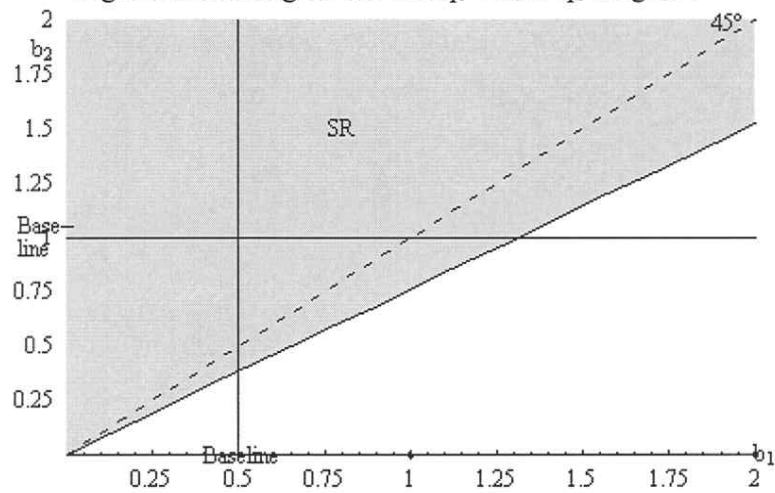
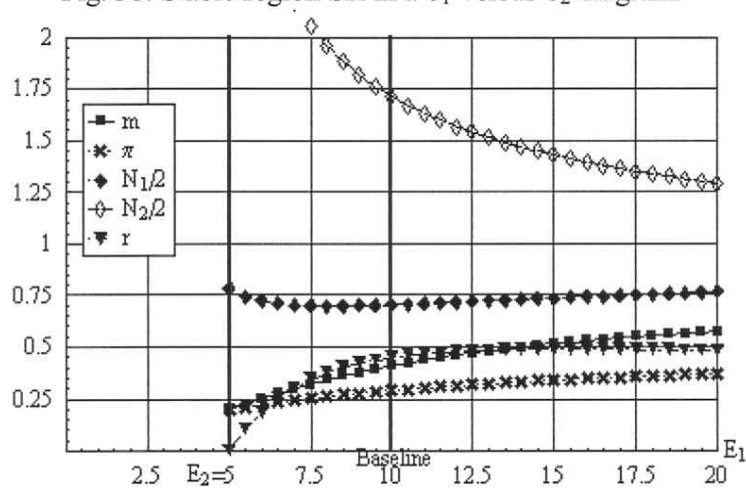


Fig. 3b. Stable region SR in a b_1 versus b_2 diagram.



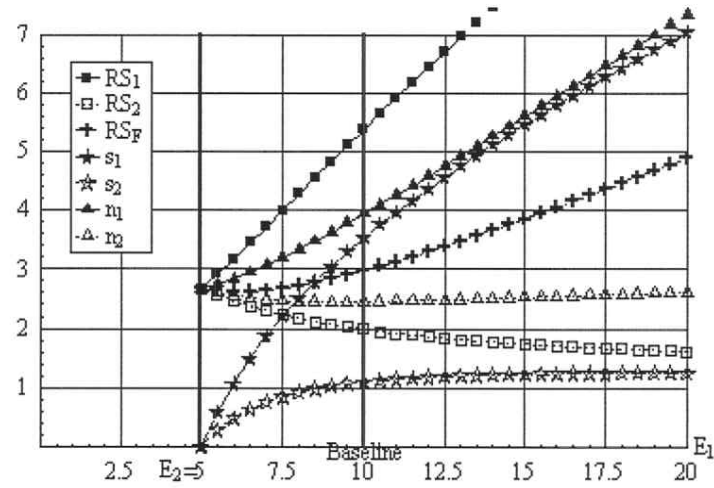


Fig. 4. Endogenous variables as functions of the H male's underlying quality (E_1).

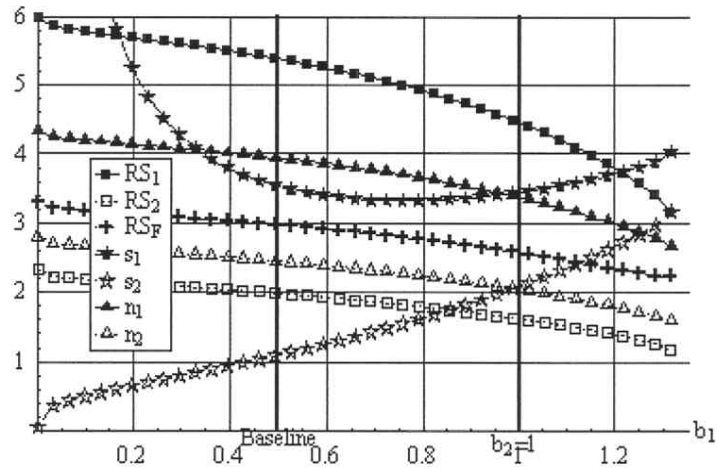
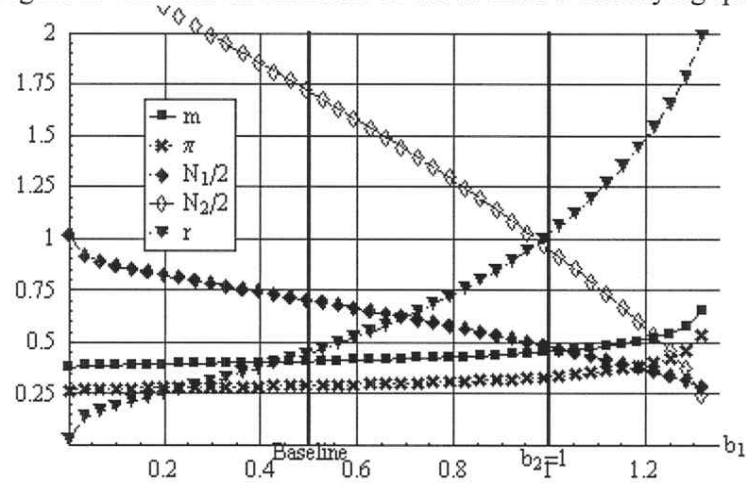


Fig. 5. Endogenous variables as functions of the H male's unit signaling cost (b_1).