Bonn Econ Discussion Papers

Discussion Paper 22/2001

Strategic Choice Handicaps when Females Pay the Cost of the Handicap

by

Georg Nöldeke, Larry Samuelson

September 2001

Bonn Graduate School of Economics
Department of Economics
University of Bonn
Adenauerallee 24 - 42
D-53113 Bonn

The Bonn Graduate School of Economics is
sponsored by the

Deutsche Post World Net
MAIL EXPRESS LOGISTICS FINANCE

STRATEGIC CHOICE HANDICAPS WHEN FEMALES PAY THE COST OF THE HANDICAP*

Georg Nöldeke
Department of Economics
University of Bonn
Adenauerallee 24–26
53113 Bonn, Germany

Larry Samuelson
Department of Economics
University of Wisconsin
1180 Observatory Drive
Madison, Wisconsin 53706-1320 USA

September 19, 2001

Abstract

We examine a strategic-choice handicap model in which males send costly signals to advertise their quality to females. Females are concerned with the *net viability* of the male with whom they mate, where net viability is a function of the male's quality and signal. We identify circumstances in which a signaling equilibrium would require high-quality males to send signals so much larger than those of males in lower quality (to deter mimicry by the latter) as to yield lower net viabilities for the former. This causes females to shun males who send large signals, ensuring that there is no signaling equilibrium.

*Financial support from the Deutsche Forschungsgemeinschaft, Graduiertenkolleg 629 at the University of Bonn, and the National Science Foundation is gratefully acknowledged.

Strategic Choice Handicaps when Females Pay the Cost of the Handicap

by Georg Nöldeke and Larry Samuelson

1 Introduction

Zahavi's ([20, 21]) handicap principle was initially regarded skeptically. For instance, Maynard Smith [15] observed that males who use a costly handicap to advertise their genetic quality offer females the prospect of offspring who will inherit not only the advantageous genetic quality but also the fitness-reducing handicap. Maynard Smith argued that the deleterious effects of the handicap were likely to overwhelm the benefit of good genes, rendering the signal ineffective as a means of revealing quality.

Grafen ([8, 9]) showed that equilibria exist in which males choose signals (i.e., handicaps) which reveal their quality. The evolutionary stability of such a signaling equilibrium hinges on the fact that signals are costly, so that low-quality males find it prohibitively expensive to mimic high-quality males. Rather than posing a fatal obstacle, the cost of a handicap is the key to its success as a means of communication.

Grafen examines a "strategic choice" handicap, in which high quality males confer a nongenetic advantage on females, such as increased fecundity ([8, p. 539], [9, p. 476]). His motivation in constructing such a model was to separate the handicap principle as a mechanism for sexual selection from forces arising out of the Fisher process (Grafen [9, pp. 473-474,484–487]). Throughout most of his analysis, higher signals impose higher fitness costs on the (higher quality) males who send them, but impose no costs on the females who mate with these males. Hence, the adverse-advertising effect that Maynard Smith identified as a threat to the handicap principle does not arise.

Subsequent work has produced numerous models showing that the handicap principle can form the basis for costly communication (see Johnstone [11] for a survey). These include models of the advertising of quality (Johnstone [10]) as well as models of the signaling of need (Godfray ([5, 6, 7]), Grafen ([8, 9]), Johnstone and Grafen ([12]), Kilner and Johnstone ([13]), Maynard Smith ([16, 17]), Nöldeke and Samuelson ([18])). These models again assume that when receivers react to signals, they are concerned only with the underlying condition of the sender and not the cost of the signal.

We follow Grafen in examining a strategic handicap model. We fill a gap in Grafen's analysis by constructing an explicitly game-theoretic model in which females are concerned with the *net viability* of the male with whom they mate, where net viability is a function of the male's quality *and* the male's signal (Grafen [8, pp.525–526]). Maynard Smith's adverse-advertising effect thus reappears, though in a different guise. In order to isolate this effect, we examine a very simple and stylized model. We derive a condition on the distribution of male qualities that is necessary and sufficient for the existence of a signaling equilibrium. When this condition is not satisfied, signaling requires that higher-quality males send much larger signals than males of lower quality, to deter mimicry by low-quality males. The signals required of high-quality males are so large as to reduce their net viability below that of lower-quality males, causing females to shun high signals and hence ensuring that males prefer not to signal. There is then no signaling equilibrium.

2 The Model

There are n males who compete for the attention of a single female. Each male i is characterized by a quality or *condition* θ_i that is independently drawn from the differentiable distribution F with support $[0, \overline{\theta}]$. This condition is not observed by other males or the female. Each male chooses a signal s_i (which may depend on θ_i), at which point the female selects one of the males with whom to mate.

A male who is not chosen by the female has fitness zero. If the female chooses a male whose condition is θ_i and signal is s_i, then the fitness of the chosen male is $\theta_i - s_i$ and the female's fitness is given by a strictly increasing function of $\theta_i - s_i$. Hence, females prefer males with high *net viability* $\theta_i - s_i$. Fecundity, for example, may be linked to the male's net viability rather than condition.

A strategy for a male is a function $s_i : [0, \overline{\theta}] \rightarrow I\!\!R_+$, with $s_i(\theta_i)$ identifying the signal the male would send if in condition θ_i. A collection of such strategies is an equilibrium if each male's strategy $s_i(\cdot)$ maximizes the male's expected fitness, given the strategies of the female and other males, and if the female chooses, from any set of male signals, the signal that maximizes her expected fitness. An equilibrium is a signaling equilibrium if each signal is send by only one condition of male, so that signals reveal their senders' conditions. We concentrate on equilibria that are strict (i.e., each agent has a unique optimal choice) and hence evolutionarily stable (Selten [19]).

A key observation is that in a signaling equilibrium, males sending larger signals must be more likely to be selected by the female, since otherwise they would not incur the extra cost of the higher signal. In addition, females "get what they want" in a strict signaling equilibrium: they can identify the characteristics of the males whose signals they observe and choose their (uniquely) preferred male, in this case the male with the highest net viability. Males sending higher signals must then have higher net viabilities, and females must choose the male sending the highest signal. In addition, males sending higher signals must be males in higher condition.

This link between high male condition and high signals characterizes any strict signaling equilibrium. Attention then turns to the question of when such equilibria exist. The essential question is whether males in higher condition send signals high enough to signal their quality without reducing their net viability. If female fitness depends only on male condition, this question is moot. If female fitness depends on net male viability, an affirmative answer is necessary for a signaling equilibrium.

3 Existence of Equilibrium

Given that females choose the highest-signaling male, our model is much like an auction, in which the males bid (signal) to be chosen by the female. It follows from standard results in auction theory that the game has a unique candidate for a strict signaling equilibrium (Fudenberg and Tirole [4, pp. 223-225], Maskin and Riley [14]). All males adopt identical, differentiable strategies, with males in higher condition sending larger signals.

To derive the males' behavior in this candidate equilibrium, notice that if $s(\theta)$ is the (common) male strategy and a male in condition θ sends the signal $s(\hat{\theta})$ for some $\hat{\theta}$, then the male's fitness is

$$(\theta - s(\hat{\theta}))F(\hat{\theta})^{n-1}, \tag{1}$$

where $(\theta - s(\hat{\theta}))$ is the net viability conditional on being chosen by the female and $F(\hat{\theta})^{n-1}$ is the probability that all other males are in condition less than $\hat{\theta}$ and hence send a signal less than $s(\hat{\theta})$ (recall that signals must be increasing in condition), causing the female to select the male in question.

To calculate the optimal signal of a male in condition θ (given the strategy $s(\cdot)$), we first differentiate (1) with respect to $\hat{\theta}$ to obtain

$$(\theta - s(\hat{\theta}))(n-1)F(\hat{\theta})^{n-2}f(\hat{\theta}) - s'(\hat{\theta})F(\hat{\theta})^{n-1}. \tag{2}$$

If $s(\theta)$ is to be an equilibrium, it must optimal for a male in condition θ to send signal $s(\theta)$, so that (2) must equal zero when $\hat{\theta} = \theta$. Rearranging the resulting equality gives

$$s(\theta)(n-1)F(\theta)^{n-2}f(\theta) + s'(\theta)F(\theta)^{n-1} = \theta(n-1)F(\theta)^{n-2}f(\theta). \quad (3)$$

Integrating both sides, we have

$$s(\theta)F(\theta)^{n-1} = \int_0^\theta (n-1)\tilde{\theta}F(\tilde{\theta})^{n-2}f(\tilde{\theta})d\tilde{\theta} \quad (4)$$

or, equivalently

$$s(\theta) = \frac{\int_0^\theta (n-1)\tilde{\theta}F(\tilde{\theta})^{n-2}f(\tilde{\theta})d\tilde{\theta}}{F(\theta)^{n-1}}, \quad (5)$$

where (4) makes use of the fact that the male in condition 0 has a zero probability of being the highest signaler, and hence optimally sends a zero signal (Grafen [8, p. 543]). In any signaling equilibrium, the signals must be given by (5). Integrating the numerator by parts allows one to verify that equilibrium signals are increasing in male condition.

As we have shown above, a signaling equilibrium exists only if males sending higher signals have higher net viability, so that it is an equilibrium for the female to select the male sending the highest signal. Equilibrium net viability is given by

$$\begin{aligned} \theta - s(\theta) &= \theta - \frac{\int_0^\theta (n-1)\tilde{\theta}F(\tilde{\theta})^{n-2}f(\tilde{\theta})d\tilde{\theta}}{F(\theta)^{n-1}} \quad (6) \\ &= \frac{\int_0^\theta F(\tilde{\theta})^{n-1}d\tilde{\theta}}{F(\theta)^{n-1}}, \quad (7) \end{aligned}$$

where (7) is obtained by performing integration by parts on the integral on the right side of (6). We thus have (see An [1] and Bagnoli and Bergstrom [2] for log concavity):

Proposition *A strict signaling equilibrium exists if and only if the expression in (7) is strictly increasing in θ, or equivalently, if and only if $\int_0^\theta F(\tilde{\theta})^{n-1}d\tilde{\theta}$ is strictly log concave in θ.*

The existence of a signaling equilibrium thus hinges upon whether the distribution of male conditions is such that $\int_0^\theta F(\tilde{\theta})^{n-1}d\tilde{\theta}$ is log concave. On the one hand, many common probability distributions have log concave

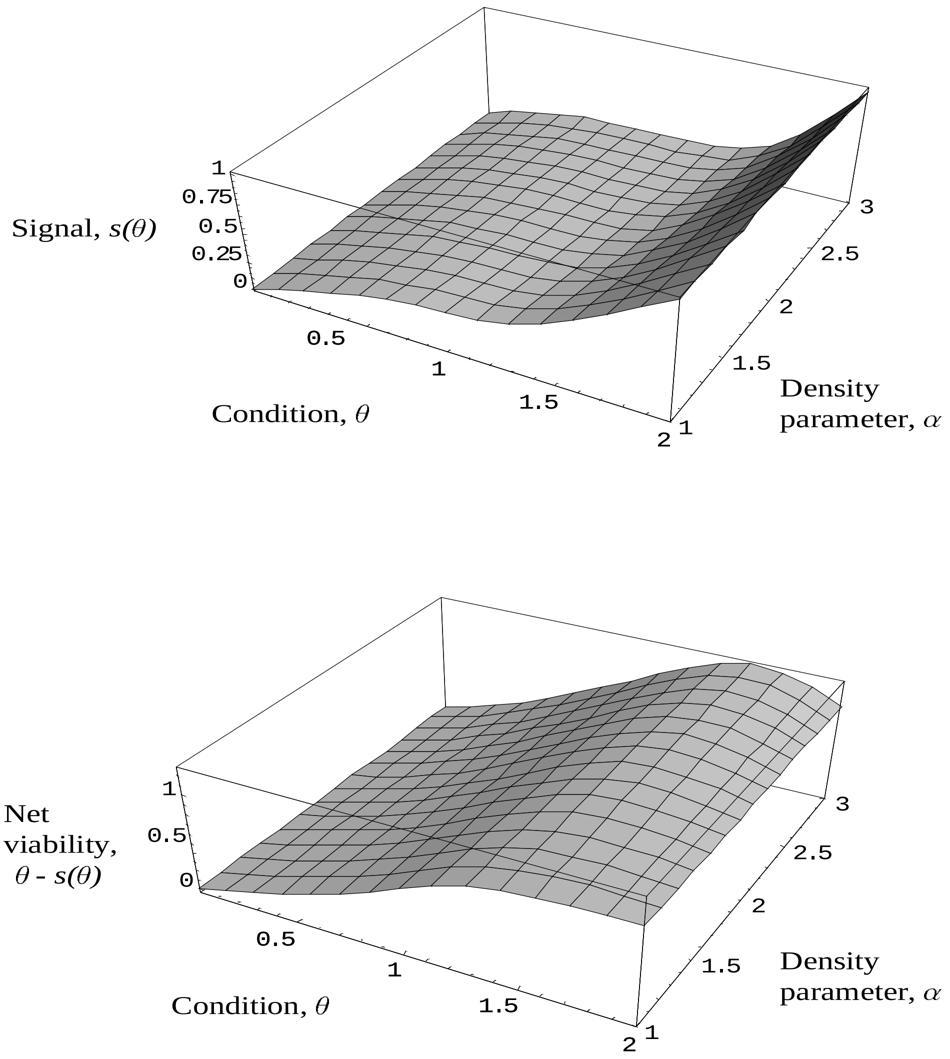

Figure 1: Illustration of a case with no signaling equilibrium. In this example, there are two males ($n = 2$) and male condition is distributed on the interval $[0, \overline{\theta}] = [0, 2]$. The distribution function F of male conditions is given by (8), where $\alpha \geq 0$ is a parameter. In any signaling equilibrium, the signaling function $s(\cdot)$ must be given by (5). The upper figure shows the signal $s(\theta)$ as a function of male condition θ and α. Males in higher condition send higher signals. The lower figure shows male net viability, given by (7), as a function of θ and α. For values of $\alpha > 1$, net viability fails to be increasing in male condition, ensuring that there is no signaling equilibrium. For example, the derivative of net viability at $\theta = 2$ is given by $(F(2)^2 - \int_0^2 F(\tilde{\theta})d\tilde{\theta} f(2))/F(2)^2 = 1 - f(2) = 1 - \frac{1}{2}(\alpha + 1)$, which is negative whenever $\alpha > 1$.

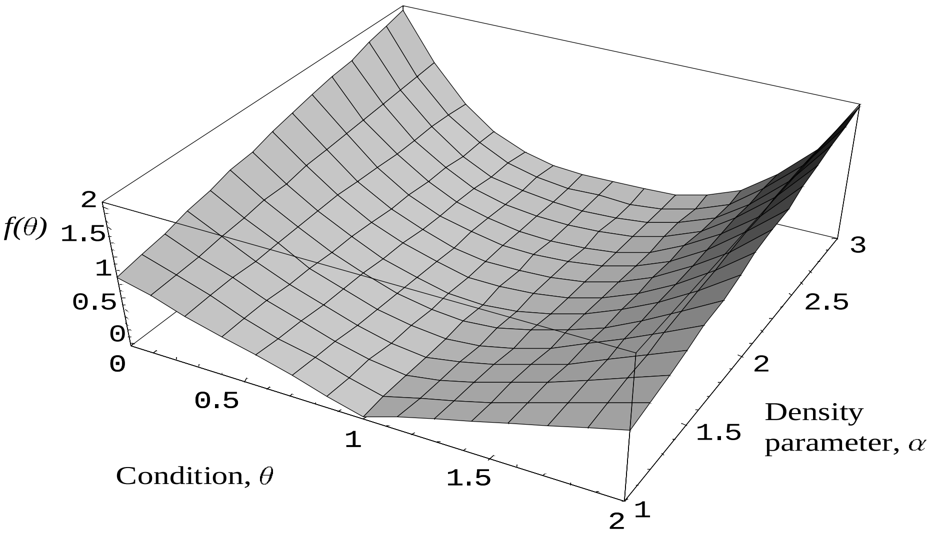

Figure 2: Density for the distribution function given in (8) and used in Figure 1. The density is given by $f(\theta) = \frac{1}{2}(\alpha+1)(1-\theta)^{\alpha}$ when $\theta \in [0,1]$ and by $f(\theta) = \frac{1}{2}(\alpha+1)(\theta-1)^{\alpha}$ when $\theta \in [1,2]$

densities (An [1], Bagnoli and Bergstrom [2]), and hence have log concave integrals of powers of their distribution functions (since log concavity is preserved by being raised to a power greater than one and by integration (An [1, Lemma 3])). However, log concavity can fail if the density concentrates its mass on males close to the lowest and highest condition. Figure 1 illustrates a case in which log concavity of the integral of the distribution function fails and hence a signaling equilibrium fails to exist.

The distribution of male condition for this example is given by

$$F(\theta) = \begin{cases} \frac{1}{2} - \frac{1}{2}(1-\theta)^{\alpha+1} & \text{if} \quad \theta \in [0,1] \\ \frac{1}{2} + \frac{1}{2}(\theta-1)^{\alpha+1} & \text{if} \quad \theta \in [1,2] \end{cases} \tag{8}$$

The density of the distribution F is shown in Figure 2. As α increases, this density increasingly concentrates its mass on males in relatively low condition and on males in relatively high condition. As a result, males in relatively high condition face stiff competition from other males in similar condition, enhancing the payoff to aggressive signaling. Males in medium condition are unlikely to face competition from others in similar condition, making it less likely that higher signals will be effective and leading to relatively modest signaling. When α is sufficiently large, these forces are powerful enough to ensure that if signals are to honestly reveal condition, then males in high condition must choose signals yielding a lower net viability than males in medium condition. But this ensures that there is no signaling equilibrium.[1]

---

[1] There always exists an equilibrium in which no signals are sent and females ignore

4 Discussion

Examining a strategic-choice handicap model in which females are concerned with net male viability, we have derived a necessary and sufficient condition for the existence of a signaling equilibrium. This condition, concerning the distribution of male qualities and ensuring that females prefer high-signaling males, is likely to be satisfied when the accompanying density is unimodal and likely to fail when it departs significantly from unimodality, such as in our example of a sharply U-shaped distribution.

We have attempted to isolate the issues surrounding signaling and net viability by examining a very simple model. If a signaling equilibrium exists in our model, whether females are concerned with male condition or with net male viability, its properties match those identified by Grafen ([8])—males in higher condition send higher signals and (in the latter but not necessarily former case) have higher net viability. If females in our model do *not* bear the cost of male advertising, then a signaling equilibrium exists. Our contribution is the demonstration that when females are concerned with net viability, the existence of a signaling equilibrium in a model of strategic handicaps cannot be taken for granted.[2]

This result is relevant for more than sexual selection. Dawkins [3] attributes to Zahavi the suggestion that prey might signal their condition to potential predators. Predator-prey interactions provide a natural setting in which the receiver's fitness depends upon both the condition and the signal of the sender, since both factors may affect the probability that the predator will be able to capture a particular prey.

References

[1] Mark Yuying An. Logconcavity versus logconvexity: A complete characterization. *Journal of Economic Theory*, 80:350–369, 1998.

---

any signals that they happen to observe. There may exist other Nash equilibria that are not evolutionarily stable in which signals are partially informative or in which males' signals reveal their types but males in different condition and sending different signals have identical equilibrium net viabilities, with the female choosing randomly among these net viabilities in the precise proportions required to support the equilibrium. Such an equilibrium is not strict and can be disrupted by drift in the female's strategy.

[2] Grafen [8] circumvents this issue by working with a "model of the [strategic] model" that implicitly assumes the existence of an equilibrium in the underlying strategic model ([9, pp. 515-516]).

[2] Mark Bagnoli and Ted Bergstrom. Log-concave probability and its applications. Mimeo, University of Michigan, 1989.

[3] R. Dawkins. *The Selfish Gene*. Oxford University Press, Oxford, 1989.

[4] Drew Fudenberg and Jean Tirole. *Game Theory*. MIT Press, Cambridge, Massachusetts, 1991.

[5] H. C. J. Godfray. Signalling of need by offspring to their parents. *Nature*, 352:328–330, 1991.

[6] H. C. J. Godfray. Evolutionary theory of parent-offspring conflict. *Nature*, 376:133–138, 1995. (1995a).

[7] H. C. J. Godfray. Signaling of need between parents and young: Parent-offspring conflict and sibling rivalry. *The American Naturalist*, 146:1–24, 1995. (1995b).

[8] Alan Grafen. Biological signals as handicaps. *Journal of Theoretical Biology*, 144:517–546, 1990. (1990a).

[9] Alan Grafen. Sexual selection unhandicapped by the Fisher process. *Journal of Theoretical Biology*, 144:473–516, 1990. (1990b).

[10] Rufus A. Johnstone. Sexual selection, honest advertisement and the handicap principle: Reviewing the evidence. *Biol. Rev.*, 70:1–65, 1995.

[11] Rufus A. Johnstone. Game theory and communication. In Lee Alan Dugatkin and Hudson Kern Reeve, editors, *Game Theory and Animal Behavior*, pages 94–117. Oxford University Press, Oxford, 1998.

[12] Rufus A. Johnstone and Alan Grafen. The continuous Sir Philip Sidney game: A simple model of biological signalling. *Journal of Theoretical Biology*, 156:215–234, 1992.

[13] Rebecca Kilner and Rufus A. Johnstone. Begging the question: Are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution*, 12 (1):11–15, 1997.

[14] Eric Maskin and John Riley. Existence and uniqueness of equilibium in sealed high bid auctions. Department of Economics Discussion Paper 407, UCLA, 1986.

[15] John Maynard Smith. Sexual selection and the handicap principle. *Journal of Theoretical Biology*, 57:239–242, 1976.

[16] John Maynard Smith. Honest signalling: The Philip Sidney game. *Animal Behavior*, 42:1034–1035, 1991.

[17] John Maynard Smith. Must reliable signals be costly? *Animal Behavior*, 47:1115–1120, 1994.

[18] Georg Nöldeke and Larry Samuelson. How costly is the honest signaling of need? *Journal of Theoretical Biology*, 197:527–539, 1999.

[19] Reinhard Selten. A note on evolutionarily stable strategies in asymmetric animal contests. *Journal of Theoretical Biology*, 84:93–101, 1980.

[20] A. Zahavi. Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, 53:205–214, 1975.

[21] A. Zahavi. The cost of honesty (Further remarks on the handicap principle). *Journal of Theoretical Biology*, 67:603–605, 1977.