

# A dynamic approach of the “Handicap Principle”

*Pierre Bernhard*<sup>1</sup>

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## Abstract

In his paper “Mate Selection —A Selection for a Handicap” [10], Amotz Zahavi gives a new explanation, now widely accepted, of a puzzle in mate selection that had already been noticed by Darwin and tentatively explained by Fisher, although that explanation was later dismissed by others. See a more complete bibliography in [10]. We give a game theoretic form to Zahavi’s argument, based upon modern game theory, and specifically the notions of signalling and bayesian equilibrium. Then we investigate how evolutionary dynamics could converge to that equilibrium. Based upon an exceedingly sketchy model, we end up with a negative conclusion, and a mechanism closer to Fisher’s argument.

## 1 Introduction

The paradox of the handicap in mate selection, called Handicap Principle since the work of Zahavi [10, 11], goes as follows. It is a common observation in many species that male characters that attract females are a handicap to the individual bearing it. Examples are, among others, large antlers of deer, brilliant colors of birds, long feathers of the peacocks’ tail, song of cicadas, etc. How did natural selection lead to the emergence of species where females would prefer handicapped males ?

A history of the related discussion, from Darwin to modern times, including Wallace—who dismissed mate selection as an evolutive device—Fisher [2], Grafen [4, 5] and Maynard Smith [7] can be found in the papers [10] and [5]. Our aim here is to use the formulation in the framework of modern game theory, and specifically of signalling theory (see [3, 8]), essentially the same as that of Grafen [5], to attempt a dynamic investigation of the associated evolutionary game. As a matter of fact, a bayesian equilibrium seems to be such a convoluted notion of equilibrium that one may wonder whether there is a mechanistic process that may have driven evolution to that state. Hence the attempt at a dynamic description in terms, here, of the replicator dynamics. This will be done here only for a very simplistic model, and the conclusion points to Fisher’s explanation more than to Zahavi’s and Grafen’s !

## 2 Signalling and bayesian equilibrium

### 2.1 A signalling game

A simple signalling game is as follows. There are two players, 1 and 2, choosing their decisions  $u_1$  and  $u_2$  in decision sets  $U_1$  and  $U_2$  respectively, most often sets of mixed strategies.

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The payoffs of the players are functions  $J_i(\theta, u_1, u_2)$ ,  $i = 1, 2$ , of the decisions and of a parameter  $\theta$  belonging to some set  $\Theta$ . But  $\theta$  is a “private information” of player 1, *i.e.* player 1 is able to choose his control via a function  $\psi_1$  as  $u_1 = \psi_1(\theta)$ , while player 2 does not know  $\theta$ .

The game goes as follows: player 1 plays first. His decision  $u_1$  creates, possibly via a noisy —probabilistic— mechanism, a *signal*  $s$  observed by player 2. Then player 2 plays, and he is allowed to choose his decision  $u_2$  via a function  $\psi_2$  as  $u_2 = \psi_2(s)$ .

Both players know the mechanism that generates  $s$  as a function of  $\theta$  and  $u_1$ , leading to a probability law  $\mathcal{P}_1(s | \theta, u_1)$  which is common knowledge. But player 2 does not know the specific realizations of the random variables involved.

Finally, we are compelled to adopt Harsanyi’s device for games of incomplete information: both players share an a priori distribution law, say  $\mathcal{P}_0$ , upon  $\theta$ .

The interesting feature of that kind of game is that in making his decision, player 1 should take into account the information about his private data that he is leaking to player 2 through his own decision.

## 2.2 Bayesian equilibrium

We now describe what we consider as an equilibrium of this game, called a *bayesian equilibrium*.

Player 2 will form a *conjecture* as to how player 1 has formed his decision, of the form  $u_1 = \chi(\theta)$ . Using that conjecture and the signal  $s$ , he will update his probability distribution over  $\theta$  according to Bayes rule, producing a conditional law  $\mathcal{P}_2(\theta | s)$ :

$$\mathcal{P}_2(\theta | s) = \frac{\mathcal{P}_1(s | \theta, \chi(\theta))\mathcal{P}_0(\theta)}{\int \mathcal{P}_1(s | \eta, \chi(\eta))\mathcal{P}_0(d\eta)}.$$

He then chooses  $u_2 = \psi_2(s)$  in such that,

$$\forall u_2 \in U_2, \quad \mathbb{E}^{\mathcal{P}_2(\theta|s)} J_2(\theta, \chi(\theta), \psi_2(s)) \geq \mathbb{E}^{\mathcal{P}_2(\theta|s)} J_2(\theta, \chi(\theta), u_2).$$

Assume that player 1 has correctly “guessed” player 2’s conjecture  $\chi$ . He then knows completely how player 2 will construct his decision. *i.e.*, the function  $\psi_2$ . He may choose his own decision  $u_1 = \psi_1(\theta)$  such that,

$$\forall u_1 \in U_1, \quad \mathbb{E}^{\mathcal{P}_1(s|\theta, \psi_1(\theta))} J_1(\theta, \psi_1(\theta), \psi_2(s)) \geq \mathbb{E}^{\mathcal{P}_1(s|\theta, u_1)} J_1(\theta, u_1, \psi_2(s)).$$

**Definition** The pair  $(\psi_1, \psi_2)$  is a *bayesian equilibrium* if, in the above construction,

$$\forall \theta \in \Theta, \quad \psi_1(\theta) = \chi(\theta).$$

In words: even knowing player 2’s conjecture  $\chi$ , player 1 cannot do better than using that same decision rule.

**Remark 1** *It is not necessary, in defining a bayesian equilibrium, to introduce a different name for player 2’s conjecture  $\chi$  and player 1’s decision rule  $\psi_1$ , since we want them to coincide. But doing so helps stress that  $\chi$  is part of player 2’s strategy. As usual, a Nash-like equilibrium can be viewed as a fixed point:  $\psi_1$  is a function  $\psi_1 = \mathcal{F}(\chi)$ , and a bayesian equilibrium should satisfy  $\mathcal{F}(\psi_1) = \psi_1$ .*

We do not attempt to write here first order necessary conditions that a bayesian equilibrium should satisfy, because we shall only need a particular, and simpler, form for our purpose. We only notice that there are bayesian equilibria where the signal  $s$  is an invertible function of  $\theta$ , so that if that equilibrium is played, after player 1 has played player 2 is actually exactly informed of the previously private information  $\theta$ . The signal is said to be “honest”. Such an equilibrium is called *separating*. Otherwise, the equilibrium is called *pooling*. Examples are easy to find where the signal is a constant, independant of the private parameter, thus revealing no information at all. And the same game may have equilibria of both types (see e.g. [8]). Mixed equilibria also exist.

### 3 Mate selection

#### 3.1 The signalling game

In the species considered, there are males and females, whose fitnesses will be denoted  $F_{\sigma}$  and  $F_{\varphi}$  respectively.

Each male has a specific *quality*, a trait measured by  $q \in \mathcal{Q} \subset \mathbb{R}$ , favourable to its overall fitness. It bears also a male phenotype related to its quality, denoted  $s \in \mathcal{S} \subset \mathbb{R}$  (for *signal*). Typically, the size of the antlers for a deer.

Upon meeting a male, a female has a probability  $m$  of accepting to mate with him. The better that male’s quality, the more usefull a large  $m$  for the female. Yet she has no other cue to a male’s quality than its signal  $s$ . And of course, a large  $m$  is favourable to the corresponding male’s fitness.

Let us formalize that situation. The fitnesses of the individuals involved are two functions

$$F_{\sigma}(q, s, m) \quad \text{and} \quad F_{\varphi}(q, m),$$

assumed twice differentiable for our purpose. The male “chooses” his signal  $s$ , based upon his private information  $q$ , as a *strategy*  $s = \psi_{\sigma}(q)$  and the female “chooses” her mating probability  $m$  with a particular male based upon the observed signal, as a strategy  $s = \psi_{\varphi}(s)$ .

The hypotheses are that

$$\frac{\partial F_{\sigma}}{\partial q} > 0, \quad \frac{\partial F_{\sigma}}{\partial m} > 0, \quad \frac{\partial^2 F_{\varphi}}{\partial q \partial m} > 0.$$

The last inequality captures the fact that for a low  $q$ , increasing  $m$  may little increase, or even decrease,  $F_{\varphi}$ , while for a large  $q$ , increasing  $m$  will strongly increase  $F_{\varphi}$ . Hence  $\partial F_{\varphi} / \partial m$  should indeed be increasing with  $q$ .

We also assume the classical concavity assumptions:

$$\frac{\partial^2 F_{\sigma}}{\partial s^2} < 0, \quad \text{and} \quad \frac{\partial^2 F_{\varphi}}{\partial m^2} < 0,$$

that let maxima exist.

### 3.2 The bayesian equilibrium

We are looking for a bayesian equilibrium, i.e. a pair of decision rules  $s = \psi_{\sigma}(q)$ ,  $m = \psi_{\varphi}(s)$ . We may, without loss of generality assume that

$$\psi'_{\sigma} = \frac{d\psi_{\sigma}}{dq} \geq 0.$$

It is a matter of choosing the definition of what is a “large”  $s$ . But we shall further assume that the inequality is strict—the male’s quality does impact its signal—, leading to a separating equilibrium.

According to the definition of the bayesian equilibrium, the female forms a *conjecture*  $s = \psi_{\sigma}(q)$ . She would like to use a strategy  $m = \varphi(q)$ . Assuming that the equilibrium is separating, she will therefore use  $m = \varphi \circ \psi_{\sigma}^{-1}(s) =: \psi_{\varphi}(s)$ . Notice that as a consequence

$$\psi'_{\varphi}(s) = \frac{\varphi'}{\psi'_{\sigma}}(\psi_{\sigma}^{-1}(s)).$$

It is clear that the optimal  $\varphi$  satisfies  $\varphi' > 0$ . This can be derived from the first order necessary condition

$$\frac{\partial F_{\varphi}(q, m)}{\partial m}(q, \varphi(q)) = 0,$$

which, via the implicit function theorem yields

$$\varphi' = -\frac{\partial^2 F_{\varphi}}{\partial q \partial m} \left( \frac{\partial^2 F_{\varphi}}{\partial m^2} \right)^{-1} > 0.$$

We now write the first order necessary condition for the optimality of  $\psi_{\sigma}$ , for  $\psi_{\varphi}$  fixed

$$\frac{\partial F_{\sigma}}{\partial s} + \frac{\partial F_{\sigma}}{\partial m} \psi'_{\varphi} = \frac{\partial F_{\sigma}}{\partial s} + \frac{\partial F_{\sigma}}{\partial m} \frac{\varphi'}{\psi'_{\sigma}} = 0. \quad (1)$$

We now know that  $\partial F_{\sigma} / \partial m > 0$ ,  $\varphi' > 0$  and  $\psi'_{\sigma} > 0$ . Hence necessarily

$$\frac{\partial F_{\sigma}}{\partial s} < 0.$$

The last inequality above is the “handicap paradox” : the signal should be detrimental to the male’s fitness, it should handicap the male. This is a general principle of signalling theory that to be credible, a signal must be “costly”. Otherwise, it is prone to deception. This has been used in other works applying signalling theory to evolutionary biology. See e.g. [4, 5], [6], [1].

Another way of writing (1) is

$$\forall q \in \mathcal{Q}, \quad \frac{dF_{\sigma}(q, \psi_{\sigma}(q), \varphi(q))}{dq} = \frac{\partial F_{\sigma}}{\partial q}(q, \psi_{\sigma}(q), \varphi(q)).$$

That is, the cost of signaling is exactly compensated for by the benefit of better mating frequency.

### 3.3 An sketchy model

The simplest model satisfying the hypotheses is as follows. Let  $\mathcal{Q} = \mathcal{S} = [0, 1]$ , and

$$F_{\mathcal{S}}(q, s, m) = q - \alpha^2 s^2 + m^2, \quad (2)$$

$$F_{\mathcal{Q}}(q, m) = -(q - m)^2. \quad (3)$$

It follows that  $\varphi(q) = q$ , and therefore that  $\psi_{\mathcal{Q}}(s) = \chi^{-1}(s)$ . The first order condition (1) reads

$$-2\alpha^2 \psi_{\mathcal{S}}(q) \psi'_{\mathcal{S}}(q) + 2q = 0.$$

Hence,  $\alpha^2 \psi_{\mathcal{S}}^2(q) = q^2 + c$ ,  $c$  an arbitrary constant. To minimize  $F_{\mathcal{S}}(q, \psi_{\mathcal{S}}(q), \varphi(q))$  but still be non-negative for all  $q \in [0, 1]$ , one must choose the constant null, and

$$\psi_{\mathcal{S}}(q) = \frac{1}{\alpha} q, \quad \psi_{\mathcal{Q}}(s) = \alpha s.$$

Placing this back in the fitness functions, we obtain

$$F_{\mathcal{S}}(q, \psi_{\mathcal{S}}(q), \psi_{\mathcal{Q}} \circ \psi_{\mathcal{S}}(q)) = q, \quad F_{\mathcal{Q}}(q, \varphi(q)) = 0.$$

## 4 Dynamics

### 4.1 Population effects of linear strategies

The strategies of both players are “closed loop” strategies, i.e. functions. Developing a replicator type of dynamics in such a set up requires to endow the set of admissible strategies—which typically we did not specify—with probability measures, and then investigate evolution equations for measures. Proving anything on these dynamics proves extremely difficult. Even the case where strategic traits are a real variable is not completely solved. (See [9]) We shall therefore greatly simplify the model (and weaken our results) in two steps.

**Step 1** We restrict the choice of strategies to linear ones. Let  $\beta, \gamma \in [0, 1]$  and

$$\psi_{\mathcal{S}}(q) = \beta q, \quad \chi(q) = \frac{1}{\gamma} q \Rightarrow \psi_{\mathcal{Q}}(s) = \gamma s.$$

Assume distributions of these coefficients among the populations of males and females respectively as time varying probability distributions  $\mathcal{P}_{\mathcal{S}}(t, \beta)$  and  $\mathcal{P}_{\mathcal{Q}}(t, \gamma)$ , independent from the quality distribution itself, governed by the probability measure  $\mathcal{P}_0$ . We also write  $\bar{\beta}$  and  $\bar{\gamma}$  for the mean values of  $\beta$  and  $\gamma$ , and  $\hat{\beta}^2$  and  $\hat{\gamma}^2$  for their mean square, and likewise for  $q$ 's mean  $\bar{q}$  and  $\hat{q}^2$  its mean square.

The fitnesses of male and female individuals is (ignoring the time argument):

$$F_{\mathcal{S}} = q + \beta^2 \left( -\alpha^2 + \int \gamma^2 \mathcal{P}_{\mathcal{Q}}(d\gamma) \right) q^2 = q + \beta^2 (\hat{\gamma}^2 - \alpha^2) q^2,$$

$$F_{\mathcal{Q}} = - \iint (1 - \beta\gamma)^2 \mathcal{P}_m(d\beta) q^2 \mathcal{P}_0(dq) = (-1 + 2\bar{\beta}\bar{\gamma} - \hat{\beta}^2 \hat{\gamma}^2) \hat{q}^2.$$

We notice that if  $\gamma$  is mismatched and different from  $\alpha$ , males have an incentive to cheat and use  $s = 1$  if  $\hat{\gamma} > \alpha$ , and give up any signalling if  $\hat{\gamma} < \alpha$ .

Assume that  $\mathcal{P}_{\text{♀}}$  has a density  $p_{\text{♀}}(t, \gamma)$ . The replicator dynamics are as follows:

$$\dot{p}_{\text{♀}}(t, \gamma) = p_{\text{♀}}(t, \gamma)[2\bar{\beta}(\gamma - \bar{\gamma}) - \hat{\beta}^2(\gamma^2 - \hat{\gamma}^2)]\hat{q}^2. \quad (4)$$

(Deriving a comparable dynamics for the males would require that we assume that different sub-population, with the *same* quality distribution, use different strategic coefficients  $\beta$ , quite unrealistic. We shall do otherwise.)

**Step 2** To make things even simpler, we assume here that females choose either of two  $\gamma$  values, say  $\gamma_1 < \alpha$  and  $\gamma_2 > \alpha$ . Let  $p_{\text{♀}}(t)$  be the proportion of the female population using  $\gamma_1$ , and therefore  $(1 - p_{\text{♀}}(t))$  the proportion using  $\gamma_2$ . Equation (4) now reads, after elementary calculations

$$\dot{p}_{\text{♀}}(t) = \hat{q}^2(\gamma_1 - \gamma_2)[2\bar{\beta} - \hat{\beta}^2(\gamma_1 + \gamma_2)]p_{\text{♀}}(t)(1 - p_{\text{♀}}(t)).$$

$\beta$  and the  $\gamma_i$ 's are no larger than 1. As a consequence,  $\beta^2 \leq \beta$ , hence  $\hat{\beta}^2 \leq \bar{\beta}$  and  $(\gamma_1 + \gamma_2) \leq 2$ . By hypothesis,  $\gamma_1 - \gamma_2 < 0$ . Therefore the coefficient in front of  $p_{\text{♀}}(1 - p_{\text{♀}})$  in the r.h.s. above is negative. Hence, for any  $p_{\text{♀}} \in (0, 1)$ , its time derivative is negative. The equilibrium probability distribution is therefore  $p_{\text{♀}} = 0$ . Then  $\hat{\gamma} \rightarrow \gamma_2 > \alpha$ , and the male population will be driven toward  $s = 1$  for all  $q$ .

**Remark** It is easy to see that the same conclusion holds if we assume that  $\gamma \in \{\gamma_1, \alpha, \gamma_2\}$ .

## 5 Conclusion

The somewhat paradoxical conclusion of this exceedingly sketchy analysis is that, while we started with Zahavi's explanation of the handicap principle, as formalized by Grafen, we end up with a dynamic system that points toward Fisher's theory of self reinforcement of female preferences, causing males to exaggerate their sexual signalling traits.

At this point, more realistic investigations are necessary, in terms of more biologically motivated fitness functions, and even more, richer strategy sets.

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