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Evolutionary dynamics of the handicap principle: an example

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Abstract

For a model developed in a companion paper, we investigate how adaptive dynamics might have led to the Bayesian equilibrium found. In an appendix, we also explain from a dynamic viewpoint a lack of equilibrium in a closely related model also invesitgated in the companion paper.

1 Introduction

Ever since Darwin, biologists interested in evolutionary biology have been puzzled by the "handicap paradox", i.e. the fact that secondary sexual characters, most often in males, that clearly attract females, be so exceedingly developed as to be a threat to the male's viability. To (over-)simplify, two mechanisms have been proposed to explain that state of affairs. One is due to Fisher [6], made into a mathematical model by Lande [10]. It is known as the "Fisher runaway". The other one, indeed much simpler, was originally proposed by Zahavi [13], and was made into a mathematical model by Grafen [9, 8]. It is known as the "handicap principle".

A notable difference is that while Fisher's runaway is a dynamical model, exhibiting a divergence as time goes to infinity, Zahavi's handicap principle describes an equilibrium, and does not say how the dynamics of evolution may have reached that equilibrium. Grafen's article [9] does contain a dynamic argument, but only in the neighborhood of the equilibrium to show its stability. (Moreover, Siller [12] has invalidated part of the dynamic argument of [9].)

In the article [1], we emphasize the exact nature of the equilibrium of the handicap paradox: a bayesian equilibrium of signaling theory, where males of different

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"qualities" signal their qualities via the secondary sexual character of interest to identical females to induce them into accepting to mate with them. In this equilibrium the performance indices are measures of the resulting fitness of the players, or a reasonable proxy of it: the expected quality of her mate for a female, and his expected number of matings for a male. Then we investigate two variants of each of two models of sexual selection directly inspired by Grafen's model [9], and in a lesser extent by Getty [7]. All four variants yield closed form bayesian equilibria. The models themselves are partly dynamical, because the behaviour of males and females depend on the time of the year, but it is an equilibrium that we compute. And because a bayesian equilibrium is a rather involved concept, it is not a priori clear how evolution may have reached it.

Our aim in this article is to provide one plausible explanation of how the dynamics of adaptation may have reached the signaling bayesian equilibrium. This is the more interesting that there actually are two bayesian equilibria in our models, one where no signaling occurs and one with a large signaling reminiscent of the observed extravagant ornaments of males of certain species.

We shall focus on the model that we deem the most interesting of all four: the "additive signaling cost" model with zero minimal male quality, and scarcity of the females as the limiting factor for the males. Concerning the "multiplicative signaling cost model" of [1], we shall only give in the appendix a dynamical explanation of an undesirable feature also found in [9].

2 The model

2.1 General description

We recall here our "additive" model and the equilibria we found. For a discussion of the underlying hypotheses and the validity of the models, and also of the implications of our solutions, we refer the reader to [1].

There is a short breeding season of length T each year, and we call $t \in [0, T]$ the time elapsed within the breeding season.

There is a fixed number $N_{♂}$ of males. The fitness of each is taken to be proportional to the number of matings he achieves over his life time. All have a potential reproduction rate large enough that they are only limited in their number of matings each season by the availability of females and the willingness of the females they meet to mate with them.

Each male has a *quality* q statistically uniformly distributed over $[0, q_1] \subset \mathbb{R}_+$.[1]

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[1] We could, without loss of generality, normalize $q_1 = 1$, taking the life expectancy of a best male that would not signal as the unit of time. For a non-unit q_1, the fitness $F_{♀}$ and $F_{♂}$, the females'

Each displays a *signal* $s \in [0, q]$, "chosen" according to a strategy $s = \psi_{♂}(q)$. Except for their quality, all males are identical and share the same strategy. The fecund life expectancy $L_{♂}$ of a male linearly increases with q, but decreases with the signal. (This last fact is the manifestation of the handicap principle. It is not hypothesized a priori, but we show in [1] under which hypotheses it is a necessary feature of the bayesian equilibrium.) More specifically, we assume that $L_{♂} = q - s$.

There is a fixed number $N_{♀}(0)$ of females at the begining of each breeding season. All females are identical. They mate only once during any breeding season. We take as a proxy of their fitness the expectation of the quality of the male they will eventually mate with. Hence they have a benefit in choosing a high quality male as a mate. This in turn puts a selective pressure on males to signal their quality q. Females cannot observe the quality of the males they meet, but only their signals. They accept a given male with a probability $m = \psi_{♀}(s, t)$, depending on the male's signal and the time during the breeding season.

Once a female has mated, she leaves the pool of available females, causing the number $n_{♀}$ of available females and its expectation $\mathbb{E}n_{♀} = N_{♀}$ to decrease, and thus the operational sex ratio $\omega = N_{♂}/n_{♀}$ to increase, during the breeding season.

Females meet fecund males in a Poisson process with a fixed intensity λ, while males meet females in a Poisson process with intensity μ. Since any such meeting involves one male and one female, one necessarily has $N_{♂}\mu = n_{♀}\lambda$, hence μ decreases according to $\mu(t) = \lambda/\omega(t)$.

We recapitulate the notation in Table 1.

2.2 The bayesian equilibrium: concept and notation

We are looking for a stable strategy pair $(s = \psi^{\star}_{♂}(q),\ m = \psi^{\star}_{♀}(s, t))$. What "stable" means is the object of signaling theory. Its concept of *bayesian equilibrium* simplifies here, for this "pure signaling game", (the signal is exactly observed by the females and does not directly impact their fitness) in the following way. (We shall use super stars to denote equilibrium strategies.)

The uninformed player, here the females, forms a *conjecture* χ about the males' strategy, meaning that they conjecture, some $s = \chi(q)$. If at equilibrium this conjecture is strictly monotonic (here increasing), the equilibrium is said to be *separating*. In that case, the females can conjecture $q = \chi^{-1}(s)$, and choose a strategy $\widehat{\psi}_{♀}(q, t)$ and play $m = \psi_{♀}(s, t) = \widehat{\psi}_{♀}(\chi^{-1}(s), t)$. A bayesian equilibrium, is one where $\psi^{\star}_{♂}$ is optimal against $(\chi, \widehat{\psi}_{♀})$, $\widehat{\psi}_{♀}$ is optimal against $\psi^{\star}_{♂}$, and $\chi = \psi^{\star}_{♂}$:

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threshold θ and the males' strategies $\psi_{♂}$ would just be multiplied by q_1. We do not do that to keep better track of the dimension of the variables involved.

T	Length of the breeding season each year.
t	Time elapsed within a breeding season.
q	Male's quality.
q_1	Maximum male quality.
s	Male's signal.
$\psi_{\male}$	Males' strategy, giving $s = \psi_{\male}(q)$.
$L_{\male}$	Male's life expectancy (in years). We have assumed $L_{\male} = q - s$.
m	Female's probability to accept to mate with a male encountered.
$\psi_{\female}$	Females' strategy giving $m = \psi_{\female}(s,t)$.
$N_{\male}$	Number of males (fixed).
$n_{\female}$	Number of available females (decreasing with t).
$N_{\female}$	Mathematical expectation $\mathbb{E}n_{\female}$.
ω	Operating sex ratio $N_{\male}/n_{\female}$.
λ	Intensity of the Poisson process of females meeting males
μ	Intensity of the Poisson process of males meeting available females.
$Q(t)$	Expected q of her future mate for a female who has not yet mated at time t.
t_m	Time at which a male of a given quality becomes "acceptable" by the females.
N_m	Male's expected number of matings per breeding season. (Function of s.)

It is convenient to use the dimensionless parameters

k	$k = 2/(\lambda T)$.
τ	$\tau = (T - t)/T$.
τ_m	$\tau_m = (T - t_m)/T$.

Table 1: The main notation used in the model

Definition 1 *A separating bayesian equilibrium is a pair* $(\psi^{\star}_{\male}, \psi^{\star}_{\female})$ *such that*

$$\psi^{\star}_{\female}(s,t) = \widehat{\psi}_{\female}((\psi^{\star}_{\male})^{-1}(s), t)\,, \qquad (1)$$

where the pair $(\psi^{\star}_{\male}, \widehat{\psi}_{\female})$ *is a Nash equilibrium of the complete information game.*

Of course, this is a construction of thought. Females are not assumed to actually "conjecture" anything, and equation (1) should be seen as a useful representation of the equilibrium strategy.

In our model, the bayesian equilibrium is a slight deviation from the above definition, in that $\psi^{\star}_{\male}$ is not strictly increasing, but yet, it provides all the needed information on q for the females to determine their optimal behaviour.

2.3 Females' behaviour

It turns out that there is a separating bayesian equilibrium, meaning that at equilibrium, females exactly infer males' quality from their signal. They adopt a threshold policy where a male is accepted if his quality is larger than the expected quality $Q^\star(t)$ of their future mate if they have not yet mated at that time.

We show in [1] that $Q^\star(t)$ obeys the differential equation

$$\dot{Q} + \lambda \mathbb{E} \max\{q - Q, 0\} = 0 \,, \quad Q(T) = 0 \,.$$

the solution of which is given by

$$Q^\star(t) = q_1 \frac{T - t}{(k+1)T - t} \,. \tag{2}$$

The a priori expected quality of her mate for any female at equilibrium is thus:

$$Q_0^\star = Q^\star(0) = \frac{q_1}{k+1} \,. \tag{3}$$

The females conjecture as to the males' strategy is $s = \chi(q)$, with $\chi(0) = 0$. Then the threshold strategy translates into

$$\theta^\star(t) = \chi(Q^\star(t))$$

and

$$m = \psi_{♀}^\star(s,t) := \begin{cases} 0 & \text{if } s < \theta^\star(t) \,, \\ 1 & \text{if } s \geq \theta^\star(t) \,. \end{cases} \tag{4}$$

2.4 Males' strategy

2.4.1 Mating opportunities

It follows that a male with a signal s mates no earlier than a time t_m given by

$$\tau_m := \frac{T - t_m}{T} = \begin{cases} 1 & \text{if } \chi^{-1}(s) \geq Q_0^\star \,, \\ k \dfrac{\chi^{-1}(s)}{q_1 - \chi^{-1}(s)} & \text{if } \chi^{-1}(s) \leq Q_0^\star \,. \end{cases} \tag{5}$$

We assume that the potential reproduction rate of all males is large enough, so that the limiting factor in their number of matings is the scarcity of available and willing females. Females dynamics as outlined above imply that the expected number of available females at any time during the breeding season is (see [1])

$$N_{♀}(t) = N_{♀}(0) \left(\frac{(k+1)T - t}{(k+1)T} \right)^2 \,. \tag{6}$$

The expected rate of males meeting available females is $\mathbb{E}\mu(t) = \lambda N_{♀}(t)/N_{♂} = \mu_0 N_{♀}(t)/N_{♀}(0)$. The expected number of matings per breeding season for a male is the integral of $\mathbb{E}\mu$ from t_m to T, i.e.

$$N_m(s) = \frac{K}{3}\left[\left(\frac{q_1}{q_1 - \chi^{-1}(s)}\right)^3 - 1\right], \tag{7}$$

with $K = \mu_0 T k^3/(k+1)^2$.

2.4.2 Males' strategies

The males fitness function is given by

$$F_{♂} = \widehat{F}_{♂}(q,s) = \frac{K}{3}(q-s)\left[\left(\frac{q_1}{q_1 - \chi^{-1}(s)}\right)^3 - 1\right]. \tag{8}$$

Equations (5) and (8) show that for $\chi^{-1}(s) > Q_0$, $\widehat{F}_{♂}$ is strictly decreasing in s, so that there is no incentive for such a male to advertise with a signal larger than for $\chi^{-1}(s) = Q_0$. For smaller qualities, we differentiate $\widehat{F}_{♂}(q,s)$ with respect to s and equate to zero. At the bayesian equilibrium, $\chi = \psi_{♂}$, and this yields a differential equation for $\psi_{♂}$, specifically

$$\psi'_{♂}(q) = q_1^3 \frac{q - \psi_{♂}(q)}{q(q_1 - q)(q_1^2 - q_1 q + \frac{q^2}{3})}, \qquad \psi_{♂}(0) = 0\,. \tag{9}$$

We show in [1] that the differential equation (9) has a closed form solution $\Psi(\cdot)$:

$$\Psi(q) = q_1 \frac{27q_1^5 q + 18q_1^4 q^2 + 9q_1^3 q^3 + 3q_1^2 q^4 - q^6}{2(27q_1^6 + q^6)} \tag{10}$$

leading to the equilibrium strategy

$$\psi^{\star}_{♂}(q) = \begin{cases} \Psi(q) & \text{if } q \le \dfrac{q_1}{k+1}\,, \\ \Psi\left(\dfrac{q_1}{k+1}\right) & \text{if } q \ge \dfrac{q_1}{k+1}\,. \end{cases} \tag{11}$$

3 Evolutionary dynamics

3.1 Fundamental hypothesis

We formulate here an hypothesis which seems reasonable, and greatly simplifies the investigation of the evolutionary dynamics, in effect uncoupling the males and females dynamics. It is based upon the remark that the females' trait of interest is a *behavioural* trait, which may evolve essentially as an ecological character, while the males' trait is a *physical* trait, evolving as a genetic character.

Hypothesis 1 *The dynamics of evolution of the females' behaviour is much faster than that of the males' signaling strategy.*

As a consequence, using Kolmogorov's theorem, if the females' behaviour dynamics turn out to be stable, we may investigate them with a constant males' strategy, and the males' strategy dynamics may be investigated with $\chi = \psi_♂$, which will prove to be the limit χ.

3.2 Females' behavioural "fast" dynamics

The fitness of a female does not depend, in our model, on the behaviour of her conspecifics, so that essentially any evolutionary dynamics are simple gradient dynamics. Assuming it is essentially an ecological process, we call u the ecological time.

3.2.1 General strategy

We assume that the females adopt a strategy $\psi_♀(s,t)$. It may have been constructed as some $\bar\psi_♀(\chi^{-1}(s),t)$ with some conjecture χ. Now, before reaching the bayesian equilibrium, if ever, χ is different from $\psi_♂$ and $\bar\psi_♀$ is different from the equilibrium strategy $\widehat{\psi}_♀$. Recall, though, that now $\psi_♂$ is assumed fixed. We may set

$$\widetilde{\psi}_♀(q,t) = \psi_♀(\psi_♂(q),t)\,.$$

This is the strategy that a female happens to play.

In both cases, we use the expected quality $Q(t)$ of her future mate for a female which has not yet mated at time t. Let $a \in \{0,1\}$ be the random boolean variable describing the choice of a female meeting a male, $a = 1$ for "accept" to mate. With $\mathbb{P}(a=1) = \mathbb{E}(a) = m$. One has :

$$Q(t) = \lambda \mathrm{d}t \mathbb{E}(aq) + (1 - \lambda \mathrm{d}t \mathbb{E}a) Q(t + \mathrm{d}t)\,, \quad Q(T) = 0\,.$$

Taking the limit as $\mathrm{d}t \to 0$, we obtain

$$\frac{\mathrm{d}Q}{\mathrm{d}t} = -\lambda \mathbb{E}[a(q - Q(t))]\,, \quad Q(T) = 0\,. \tag{12}$$

We consider two cases, depending on whether females use a mixed strategy, with $m \in [0,1]$, or whether they use a threshold strategy, with $m \in \{0,1\}$, more specifically $m = 1$ if $s \geq \theta(t)$ for some time dependent threshold $\theta(t)$.

3.2.2 Mixed strategies

In this case, each female adopts a mixed strategy, i.e. she randomizes a, choosing its probability $m = \widetilde{\psi}_{♀}(q,t)$ of being 1, which is also its expected value, and with $a - m$ independent from q, as is customary for a mixed strategy. It follows that $\mathbb{E}[(a-m)q] = \mathbb{E}(a-m)\mathbb{E}q = 0$. Therefore

$$\mathbb{E}(aq) = \mathbb{E}(mq) = \int_0^{q_1} \widetilde{\psi}_{♀}(q,t)\frac{q\mathrm{d}q}{q_1}\,.$$

Now, Q obeys the differential equation

$$\frac{\mathrm{d}Q}{\mathrm{d}t} = -\lambda\mathbb{E}[\widetilde{\psi}_{♀}(q,t)(q-Q)]\,. \tag{13}$$

Let $\mathrm{D}Q(t)$ be the Fréchet derivative of $Q(t)$ with respect to $\widetilde{\psi}_{♀}$. We evaluate the variation $\delta Q(t) = \langle \mathrm{D}Q(t), \delta\widetilde{\psi}_{♀}\rangle$ for a given variation $\delta\widetilde{\psi}_{♀}$. It satisfies:

$$\frac{\mathrm{d}\delta Q}{\mathrm{d}t} = \lambda\mathbb{E}\widetilde{\psi}_{♀}(q,t)\delta Q - \lambda\int_0^{q_1}\delta\widetilde{\psi}_{♀}(q,t)(q-Q)\frac{\mathrm{d}q}{q_1}\,,$$

The first variation of the females' fitness is therefore obtained as a function of

$$h(v,u) = \exp\left(\lambda\int_u^v \mathbb{E}\widetilde{\psi}_{♀}(q,t)\,\mathrm{d}t\right)$$

as

$$\delta Q(0) = \lambda\int_0^T\int_0^{q_1} h(0,t)\delta\widetilde{\psi}_{♀}(q,t)(q-Q(t))\,\frac{\mathrm{d}q}{q_1}\,\mathrm{d}t\,, \tag{14}$$

exhibiting the gradient at q as the function $t \mapsto h(0,t)(q-Q(t))$.

Let M be the positive *mutation intensity factor* (see [2]). Finally, the adaptive dynamics are just

$$\frac{\mathrm{d}\widetilde{\psi}_{♀}(q,t)}{\mathrm{d}u} = \begin{cases} [Mh(0,t)(q-Q(t))]_- & \text{if } \widetilde{\psi}_{♀}(q,t) = 1\,, \\ Mh(0,t)(q-Q(t)) & \text{if } \widetilde{\psi}_{♀}(q,t) \in (0,1)\,, \\ [Mh(0,t)(q-Q(t))]_+ & \text{if } \widetilde{\psi}_{♀}(q,t) = 0\,. \end{cases}$$

They lead to

$$\frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{\mathrm{d}Q(t)}{\mathrm{d}u}\right) = \lambda\mathbb{E}[\widetilde{\psi}_{♀}(q,t)]\frac{\mathrm{d}Q(t)}{\mathrm{d}u} - \lambda h(0,t)\mathbb{E}[M(q-Q(t))^2]$$

if $\mathrm{d}\widetilde{\psi}_{♀}/\mathrm{d}u \neq 0$, with

$$\frac{\mathrm{d}Q}{\mathrm{d}u}(T) = 0\,.$$

Now, the semi-group $h(\cdot,\cdot)$ is positive. Hence $\mathrm{d}Q(t)/\mathrm{d}u > 0$, pointing to a constantly increasing $Q(t)$. But $Q(t)$ is bounded above by $Q^\star(t)$. Therefore $Q(t)$ converges, uniformly according to Dini's theorem, to some $\widehat{Q}(t)$, and $\widetilde{\psi}_{♀}(q,t)$ converges to

$$\widetilde{\psi}_{♀}(q,t) = \left\{ \begin{array}{ll} 0 & \text{if } q < \widehat{Q}(t)\,, \\ 1 & \text{if } q \geq \widehat{Q}(t)\,. \end{array} \right. \tag{15}$$

Because of the continuity of the solution of an ordinary differential equation with respect to its right-hand side, it follows that $\widehat{Q}(t) = Q^\star(t)$, and the limiting strategy (15) coincides with the equilibrium strategy

$$\psi^\star_{♀}(s,t) = \left\{ \begin{array}{ll} 0 & \text{if } s < \psi_{♂}(Q^\star(t))\,, \\ 1 & \text{if } s \geq \psi_{♂}(Q^\star(t))\,. \end{array} \right.$$

3.2.3 Threshold strategy

We now consider the case where the females' strategy evolves from the start as a threshold strategy. Let it be

$$\psi_{♀}(s,t) = \left\{ \begin{array}{ll} 0 & \text{if } s < \theta(t)\,, \\ 1 & \text{if } s \geq \theta(t)\,. \end{array} \right.$$

We set $\check{q}(t) = \psi_{♂}^{-1}(\theta(t))$, so that the same strategy can be expressed as

$$\widetilde{\psi}_{♀}(q,t) = \left\{ \begin{array}{ll} 0 & \text{if } q < \check{q}(t)\,, \\ 1 & \text{if } q \geq \check{q}(t)\,. \end{array} \right.$$

In equation (12), we now have $a = 1$ if $q \geq \check{q}$, and $\mathbb{E}(aq) = \mathbb{E}a\mathbb{E}(q \mid a = 1)$, i.e. $\mathbb{E}(aq) = \mathbb{P}(q \geq \check{q})\mathbb{E}(q \mid q \geq \check{q})$. The expected mate's quality now obeys

$$\frac{\mathrm{d}Q}{\mathrm{d}t} = -\lambda \mathrm{d}t \left(\frac{q_1 - \check{q}}{q_1}\right)\left(\frac{q_1 + \check{q}}{2} - Q\right)\,, \quad Q(T) = 0\,.$$

We compute its gradient with respect to $\check{q}(\cdot)$. Let $\delta Q(t) = \langle \mathrm{D}Q(t), \delta\check{q}\rangle$. It obeys

$$\frac{\mathrm{d}\delta Q}{\mathrm{d}t} = \lambda\frac{q_1 - \check{q}}{q_1}\delta Q - \frac{\lambda q_1}{q_1}(Q - \check{q})\delta\check{q}\,, \quad \delta Q(T) = 0\,.$$

Let

$$g(v,u) = \exp\left(\lambda\int_u^v \frac{q_1 - \check{q}(t)}{q_1}\mathrm{d}t\right)\,.$$

We obtain

$$\delta Q(0) = \lambda \int_0^T g(0,t)(Q(t) - \check{q}(t))\,\mathrm{d}t\,.$$

Thus, the gradient is of the sign of $Q - \check{q}$. We conclude as above that the adaptive dynamics

$$\frac{\mathrm{d}\check{q}(t)}{\mathrm{d}u} = Mg(0,t)(Q(t) - \check{q}(t))$$

make $Q(t)$ converge monotonically, hence uniformly, toward $Q^\star(t)$ while the threshold $\check{q}$ converges toward $\check{q}(t) = Q^\star(t)$ for all t, and that this generates the same equilibrium strategy as previously. We have therefore proved the following:

Theorem 1 *Whether they use mixed strategies or threshold strategies, the females' behaviour converges toward the signaling equilibrium threshold strategy.*

Therefore, in the limit, females behave *as if* they were making the right conjecture about the males' strategy.

3.3 Males' strategic "slow" dynamics

3.3.1 Adaptive dynamics

It follows from the hypothesis 1 and from the previous subsection that we may investigate the males' strategy dynamics as if $\chi = \psi_{♂}$ and the females use the threshold $q = Q^\star$. Let v denote evolutionary time.

For lack of a better choice, we shall make use of the adaptive dynamics approach (see [2]), although it has been completely justified [11, 5, 3] in the case of clonal reproduction, while we investigate sexual behaviour. One possible hypothesis to better fit the theoretical framework of adaptive dynamics would be to assume that the trait considered is inherited from the father only (say on the Y chromosome of mammals, but this does not account for birds). But we do not wish to insist on this justification, simply taking adaptive dynamics for a plausible description of evolution. In so doing, we shall also assume that *the mutation intensity is independent of the quality*.

Let $\psi_{♂}$ be the resident strategy among males. At equilibrium, thus, $\chi = \psi_{♂}$. Assume a mutation produces a small deviation away from that strategy in some males. The fitness of the mutants depends on the resident strategy through the females' behaviour according to their "conjecture" $\chi = \psi_{♂}$. If this fitness is larger than the resident's, this strategy will invade and, with the males' population dynamics, replace the resident strategy. Then the females' behaviour will adapt again. Accordingly, the dynamics of the trait $\psi_{♂}(\cdot)$ will be obtained by taking the gradient of the males' fitness with respect to the signal, assuming the females' conjecture $\chi(\cdot)$ fixed at the resident value of $\psi_{♂}(\cdot)$.

Since this trait is function valued, this will yield a partial differential equation, as emphasized in [4]. As compared to the treatment there, beyond the mathematical difficulties[2] raised by the definition of their $\sigma^2(q', q)$, in such a general framework as ours we have no ground to postulate a specific cross-correlation between different values of q. Therefore, we neglect any such effect and choose to ignore it, or, equivalently, set $\sigma^2(q', q) = \delta(q - q')$. (Note that this is essentially what the authors do in the examples provided in the article.)

3.3.2 Mathematical analysis

According to the above analysis, we differentiate $F_{♂}(q, s, \psi^{\star}_{♀}(s))$ with respect to s assuming $\chi(\cdot)$ fixed at $\chi = \psi_{♂}$. Call v the evolutionary time, and denote $\psi'_{♂} = \partial\psi_{♂}(q, v)/\partial q$. Assume a constant mutation factor M. We obtain

$$\frac{\partial\psi_{♂}(q, v)}{\partial v} = \frac{KM}{(q_1 - q)^3}\left[q_1^3 \frac{q - \psi_{♂}}{(q_1 - q)\psi'_{♂}} - q_1^2 q + q_1 q^2 - \frac{q^3}{3}\right]. \tag{16}$$

The problem now is to investigate the asymptotic behaviour of the solution of this partial differential equation (PDE) as v goes to infinity, for any positive, supposedly small, initial condition $\psi_{♂}(q, 0)$, and for $q \in [0, Q_0]$.

We were not able to *prove* conclusively its convergence toward the equilibrium strategy. However it is clear that it does in view of the following development.

We claim:

Theorem 2 *In equation (16), let $\psi_{♂}(0, 0) = 0$, $p_0 \in (0, 1/2)$ and, $\forall q \in [0, Q_0^{\star}]$, $\psi'_{♂}(q, 0) \in [p_0, 1/2]$. Then, if $\psi_{♂}(\cdot, v)$ converges in that range as $v \to \infty$, it is toward Ψ, given by equation (10).*

Proof Note first the following:

Proposition 1 *If the solution of (16) converges for $q \in [0, Q_0^{\star}]$ as $v \to \infty$, it is either toward the trivial equilibrium $\psi_{♂}(\cdot, \infty) = 0$ or toward the signalling equilibrium solution $\psi_{♂}(\cdot, \infty) = \Psi(\cdot)$ (10).*

Proof Indeed, for any limit, the right-hand side of (16) must be either zero, meaning that $\psi_{♂}(\cdot, \infty) = \Psi(\cdot)$, or indeterminate, which happens only on the trivial equilibrium solution $\psi_{♂}(q) = 0$.

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[2] The fact that x and x' in equation (2) of [4] belong to a Banach space makes it very difficult to give a meaning to $M(x', x)$ and to the integral: the symbol $\mathrm{d}x'$ cannot stand for the Lebesgue measure which does not exist in a Banach space.

Lemma 1 *Under the hypotheses of the theorem, the solution of equation (16) cannot converge to* $\psi_{\male}(q) = 0$.

Proof We write the equations of the characteristic curves of equation (16), using the classic notation $\psi'_{\male} = p$. They read

$$\begin{aligned}
\frac{\mathrm{d}q}{\mathrm{d}v} &= KMq_1^3 \frac{q - \psi_{\male}}{p^2(q_1 - q)^4}\,, && (17)\\
\frac{\mathrm{d}\psi_{\male}}{\mathrm{d}v} &= KM \frac{1}{(q_1 - q)^3}\left(2q_1^3 \frac{q - \psi_{\male}}{p(q_1 - q)} - q_1^2 q + q_1 q^2 - \frac{q^3}{3}\right)\,, && (18)\\
\frac{\mathrm{d}p}{\mathrm{d}v} &= KM \frac{q_1^3}{(q_1 - q)^4}\left(4\frac{q - \psi_{\male}}{p(q_1 - q)} + \frac{1}{p} - 2\right)\,. && (19)
\end{aligned}$$

Note that $q(v) = 0$, $\psi_{\male}(q(v)) = 0$ is a characteristic curve. Then, we claim:

Proposition 2 *The solution of (16) satisfies for all* $q \in [0, Q_0^\star]$, $\psi_{\male}(q, v) < q$.

Proof It follows from equations (17) and (18) that (we denote with a dot differentiation with respect to v)

$$(q - \psi_{\male})^{\cdot} = \frac{KMq_1^3}{(q_1 - q)^3}\left(\frac{1 - 2p}{p^2(q_1 - q)}(q - \psi_{\male}) + \frac{q}{q_1} - \frac{q^2}{q_1^2} + \frac{q^3}{3q_1^3}\right)\,,$$

with $q(0) - \psi_{\male}(q(0), 0) > 0$. Because $q/q_1 < 1$, the last three terms in the right hand side above add to a positive value. Let $a(v) = KMq_1^3(1-2p)/(p^2(q_1-q)^4)$. By the theorem of comparison of the solutions of ordinary differential equations, we have $q - \psi_{\male}(q, v) > y(v)$ where $y(v)$ is the solution of the differential equation

$$\dot{y} = a(v)y\,, \quad y(0) = q(0) - \psi_{\male}(q(0), 0) > 0\,,$$

as long as $q < Q_0^\star < q_1$. Therefore $y(v)$ remains positive for all relevant v, proving the proposition.

Proposition 3 *The characteristic curves fill a neighborhood of the* v *axis in the* (v, q) *plane.*

Proof To use the local surjectivity theorem, check that the differential

$$\delta q(v) = \frac{\mathrm{d}q(v)}{\mathrm{d}q(0)}\delta q(0) + \frac{\mathrm{d}q(v)}{\mathrm{d}\psi_{\male}(0)}\delta\psi_{\male}(0, 0)$$

remains positive for all v, provided that $\delta q(0) - \delta\psi_{\male}(0,0) > 0$. This last inequality and the previous proposition guarantee that the differentials satisfy $\delta q(v) - \delta\psi_{\male}(0,v) > 0$, driving the variational equation

$$\delta\dot{q}(v) = \frac{1}{p^2(v)}(\delta q(v) - \delta\psi_{\male}(0,v))\,, \quad \delta q(0) > 0\,,$$

to positive values.

We now prove the lemma. Indeed, the characteristic equation for p along the characteristic $q(v) = 0$, $\psi_{\male}(0,v) = 0$ is

$$\dot{p} = \frac{KM}{q_1}\left(\frac{1}{p} - 2\right). \tag{20}$$

Hence, as long as $p < 1/2$, it is increasing. Hence for all v, $p(v) > p_0$. By continuity, there is a neighborhood of the v axis of the (v,q) plane where $p(v) > p_0/2$. Hence in that neighborhood $\psi_{\male}(q,v) \geq p_0 q/2$, forbidding a convergence of $\psi_{\male}(q,v)$ toward zero. This proves the lemma, and together with proposition 1, the theorem.

3.3.3 Further evidence

We have not conclusively *proved* that for all $q \in [0, Q_0^\star]$, the solution $\psi_{\male}(q,v)$ of equation (16) converges toward $\Psi(q)$, solution of $\partial\psi_{\male}(q,v)/\partial v = 0$, i.e. toward $\Psi(q)$. Yet we offer two other indications.

On the characteristic curve $q(v) = 0$, $\psi_{\male}(0,v) = 0$, $p(v)$ is governed by equation (20), from which it follows that $p(v) \to 1/2 = \mathrm{d}\Psi/\mathrm{d}q(0)$. Moreover, we were able to prove mathematically that the second derivative $(\partial^2\psi_{\male}/\partial q^2)(0)$ converges to $2/3$, the second derivative of $\psi_{\male}^\star$.

More convincingly, we used the characteristic equations (thus getting around a severe numerical instability of the finite difference method) with a Runge Kutta method of order 4 to integrate equation (16) from $\psi_{\male}(q,0) = 0.1q$, obtaining numerical approximations of $\psi_{\male}(q,v)$ for various values of v. Using $q_1 = 1$, and arbitrarily, $KM = 10^{-3}$, the results up to $v = 1000$ appear in Table 2 together with $\psi_{\male}^\star$. For $v = 1500$, the difference with $\psi_{\male}^\star$ is below 5×10^{-5}. The precision of the approximation of $\psi_{\male}^\star$ is the more striking that the characteristic curves themselves do not stabilize as $v \to \infty$.

Figure 1 shows the graphs of $\psi_{\male}(q,v)$ for various values of v. The graph for $v = 1000$ is indistinguishable from that of $\psi_{\male}^\star$.

q	$v=0$	$v=5$	$v=10$	$v=100$	$v=1000$	$\psi^{\star}_{\male}$
$0,1$	$0,01$	$0,0145$	$0,0175$	$0,0370$	$0,0533$	$0,0535$
$0,2$	$0,02$	$0,0322$	$0,0395$	$0,0833$	$0,1144$	$0,1148$
$0,3$	$0,03$	$0,0550$	$0,0684$	$0,1420$	$0,1846$	$0,1849$
$0,4$	$0,04$	$0,0859$	$0,1079$	$0,2167$	$0,2650$	$0,2653$
$0,5$	$0,05$	$0,1303$	$0,1644$	$0,3113$	$0,3570$	$0,3571$
$0,6$	$0,06$	$0,1987$	$0,2498$	$0,4274$	$0,4614$	$0,4615$
$0,7$	$0,07$	$0,3140$	$0,3855$	$0,5610$	$0,5791$	$0,5791$
$0,8$	$0,08$	$0,5188$	$0,5975$	$0,7038$	$0,7097$	$0,7097$

Table 2: Numerical values of $\psi_{\male}(q,v)$ obtained with the method of characteristics, and a fourth order Runge Kutta integration scheme and a fixed step size of 1.

4 Conclusion

Our analysis is entirely dependent on our hypothesis of separation of time scales between the dynamics of behavioural adaptation of females and that of physical evolution of males.

Under that hypothesis, the natural evolutionary dynamics of the females' behaviour converge toward the signalling equilibrium behaviour under two hypotheses on the nature of this behaviour during adaptation : mixed strategy or threshold strategy. That is, in the limit, females behave *as if* they had *conjectured* the right strategy of males.

Concerning the males, we feel that we have shown that indeed, for the model of sexual selection emphasized here, adaptive dynamics do converge toward the signaling equilibrium we have analyzed in our previous article [1].

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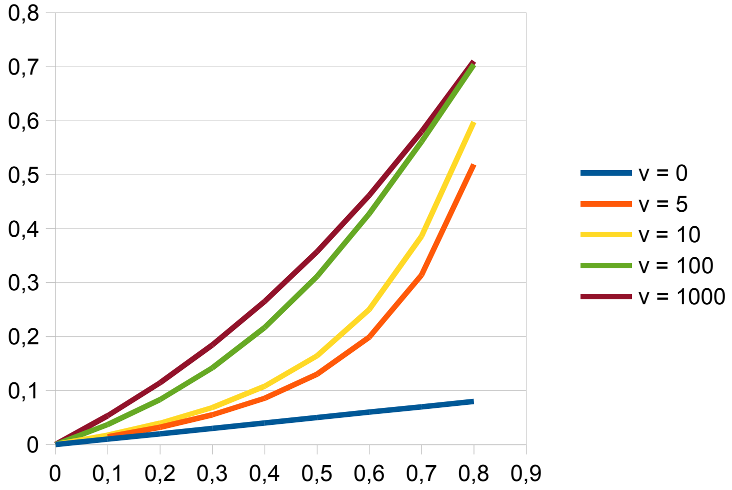

Figure 1: graph of $\psi_{\male}(q, v)$ as computed by the method of characteristics. The graph for $\psi^{\star}_{\male}$ is indistinguishable from that for $v = 1000$.

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A Appendix: Multiplicative model

In our article [1], we investigated another model [3], closer to Grafen's, that we called "multiplicative" (as opposed to the "additive" model investigated here) where we called σ a dimensionless signal, and assume $L_{♂} = q(1-\sigma)$. We concluded that that model is less satisfactory on two counts. On the one hand, it yields an excessively large equilibrium signal, and thus an exceedingly small residual survivorship at equilibrium, and, on the other hand, in that model it is not possible to let q range over $(0, q_1]$ as we did here. One has to assume a positive minimum q_0. As q_0 approaches zero, the equilibrium male signaling strategy goes to 1 for all positive q, an absurd conclusion. Yet, as low quality males may die before reaching adulthood, there is no reason why the adult life expectancy could not be arbitrarily small.

Beyond the tentative explanation given in [1] of why this undesirable feature arises, we provide here a dynamic viewpoint:

Theorem 3 *In the multiplicative model with $q_0 = 0$, no equilibrium is possible with any males' strategy $\sigma = \varphi_{♂}(q)$ with a strictly increasing $\varphi_{♂}(\cdot)$.*

Proof We may, without loss of generality, assume that $\varphi_{♂}(0) = 0$, since any other choice could lead to a translated signaling strategy conveying exactly the same information but "cheaper" in terms of loss of viability.

Females' behaviour and formula (7) (substituting σ to s) remain unchanged from the additive model, but now $F_{♂} = q(1-\sigma)N_m(\sigma)$. We differentiate it with respect to σ assuming $\chi(\cdot)$ fixed and equal to $\varphi_{♂}(\cdot)$. We write everything in terms of $r = q/q_1$. We obtain

$$\frac{\mathrm{d}F_{♂}}{\mathrm{d}\sigma} = K\left[\frac{1-\sigma}{\varphi'_{♂}} - r(1-r)(1-r+\frac{r^2}{3})\right].$$

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[3] For both models, we also investigated the case where the limiting factor for the males is their potential reproduction rate.

We wish to allow for arbitrarily large, and if necessary infinite, slope for $\varphi_{♂}$. One way of achieving this will be to use its inverse function $q = R(\sigma)$. Recalling that $r \leq 1$, we have

$$\frac{\mathrm{d}F_{♂}}{\mathrm{d}\sigma} > K(1-\sigma)\left(R'(\sigma) - \frac{R(\sigma)}{1-\sigma}\right) .$$

The coefficient $(1-\sigma)$ is always positive. Moreover, the function R is increasing. It follows that

$$\int_0^{\varsigma} \left(R'(\sigma) - \frac{R(\sigma)}{1-\sigma}\right) \mathrm{d}\sigma > R(\varsigma)[1 + \ln(1-\varsigma)],$$

which is positive for $\varsigma < 1 - \mathrm{e}^{-1}$.

Hence, in every right neighborhood of $\sigma = 0$, there are σ values, and hence also in any right neighborhood of $q = 0$ values of q, for which $\mathrm{d}F_{♂}/\mathrm{d}\sigma$ is strictly positive. These individuals would therefore have an incentive to deviate from $\varphi_{♂}$, preventing the existence of an equilibrium.