

# Games of sexual selection: static and dynamic aspects

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**Grafen’s formalization** Grafen (1990) offers a mathematical formulation of Zahavi’s principle. We shall develop two models very similar to Grafen’s, but more explicit. We offer an explanation, and a remedy, to an undesirable feature of Grafen’s model. Finally we sketch a dynamic approach of that static result.

## Pure signalling game

A *pure signaling game* is a particular, simple, case of a *signaling game*.

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**Bayesian equilibrium:** Player 2 forms a *conjecture*  $s = \chi(q)$ , and uses it to infer a *belief* on  $q$  (probabilist or sharp). With this he can maximize  $\mathbb{E}F_2(q, m)$  by playing  $m = \psi_2^*(s)$ .

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**Definition** The pair  $(\psi_1^*, \psi_2^*)$  is a *Bayesian equilibrium* if  $\psi_1^*(\cdot) = \chi(\cdot)$ .

## Separating vs pooling bayesian equilibrium

If at equilibrium,  $\psi_1^* = \chi$  is strictly monotonous, then Player 2's belief is exact :  $q = \chi^{-1}(s)$ . The equilibrium is called **separating** or **revealing**. Otherwise, the equilibrium is said **pooling**.

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As many signalling games, our's will have both a (sufficiently) separating and a pooling equilibrium: the trivial equilibrium where no signalling occurs.

For a separating equilibrium, let  $m = \hat{\psi}_2(q)$  maximize  $F_2(q, m)$ . Then,  $\psi_2^*(s) = \hat{\psi}_2(\chi^{-1}(s))$ . Hence, at equilibrium where  $\chi(\cdot) = \psi_1^*(\cdot)$ ,

$$\psi_2^{*'}(s) = \hat{\psi}_2'(\psi_1^{*-1}(s)) \frac{1}{\psi_1^{*'}(\psi_1^{*-1}(s))}.$$

The first order condition on  $F_1(q, s, \psi_2^*(s))$  yields a differential equation on  $\psi_1^*$ .

## Handicap principle

Assume that all functions are differentiable, and that at equilibrium both  $s$  and  $m$  are in the interior of their respective domains.

Assume also that the signal is “devised” to induce a favourable response from Player 2, i.e.

$$\frac{\partial F_1}{\partial m} \frac{\partial \psi_2^*}{\partial s} > 0.$$

Optimization of  $F_1$  implies

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Hence

$$\frac{\partial F_1}{\partial s} < 0.$$

**The signal has to be costly to Player 1.**



## Sexual selection “game”

Males have different qualities  $q \in [q_0, q_1] \subset \mathbb{R}_+$ .  $q_0 \geq 0$ .

They signal their quality with a signal  $s = \psi_{\sigma}(q)$ .

They have a life expectancy (or survivorship)  $L_{\sigma}(q, s)$ .

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**Females** are all identical. They mate only once per breeding season.

Hence the number  $n_{\sigma}(t)$  of available females decreases.  $\mathbb{E}n_{\sigma} = N_{\sigma}$ .

They meet males in a Poisson process of intensity  $\lambda$ .

They observe  $s$  and decide a probability  $m = \psi_{\sigma}(s)$  of accepting to mate.

They aim to maximize  $F_{\sigma} = Q(0)$ , the expected quality of their mate.

## Models and variants

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### Two variants each:

- 1) Males limited by their potential reproduction rate  $\Rightarrow \mu = \text{constant}$ .
- 2) Males limited by the scarcity of females  $\Rightarrow \mu(t) = \lambda n_{\text{♀}}(t) / N_{\sigma}$ .

## Females' behaviour

Let  $Q(t)$  be the expected quality of her mate for a female that has not yet mated at time  $t \in [0, T]$ .

$$Q(t) = \mathbb{E}[\lambda dt m q + (1 - \lambda dt m)Q(t + dt)].$$

In the limit as  $dt \rightarrow 0$ , this yields

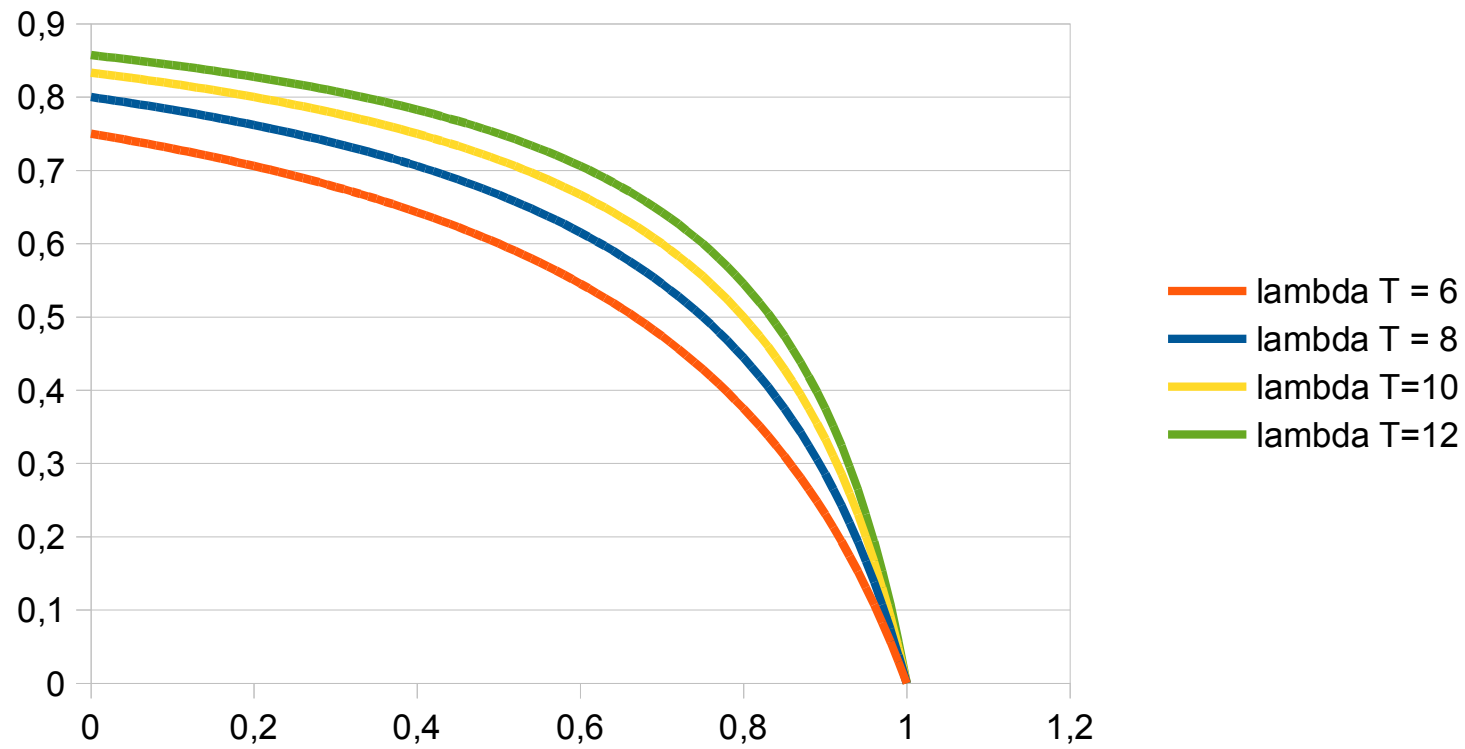
$$\frac{dQ}{dt} + \lambda \mathbb{E}[m(q - Q(t))] = 0, \quad Q(T) = 0.$$

Females' fitness  $Q(0)$  maximized by

$$m = \hat{\psi}_{\text{♀}}(q, t) = \begin{cases} 0 & \text{if } q < Q(t), \\ 1 & \text{if } q \geq Q(t), \end{cases} \Rightarrow \psi_{\text{♀}}^*(s, t) = \begin{cases} 0 & \text{if } s < \chi(Q(t)), \\ 1 & \text{if } s \geq \chi(Q(t)). \end{cases}$$

Easy to integrate in closed form if  $\mathbb{P}_0$  uniformly distributed over  $[q_0, q_1]$ .

## Curves $Q(t)$



$Q(t)/q_1$  as a function of  $t/T$  for  $q_0 = 0$ , for various values of  $\lambda T$ .



## Evolutionary dynamics ♀

**Hypothesis** The females' behaviour is a **behavioural trait**, with an adaptation must faster than the males' **physical trait**. (~ Ecological vs genetic.)

⇒ the evolution of Females' behaviour may be studied *as if*  $\psi_{\sigma}$  were fixed.

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Because a female's fitness does not depend on her conspecifics' behaviour, evolutionary dynamics are a gradient dynamics for  $F_{\text{♀}} = Q(0)$ .

$\Rightarrow$  Easy to show convergence, for two scenarii (function-valued trait):

**Mixed strategy:**  $\psi_{\text{♀}}(s, t) = m \in [0, 1]$ .

**Threshold strategy:**  $\psi_{\text{♀}}(s, t) = \Upsilon(s - \theta(t))$ .

Both evolve toward equilibrium threshold strategy.

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Males obtain a fitness  $F_{\text{♂}}(q, s, \psi_{\text{♀}}^*(s, \cdot)) = L_{\text{♂}}(q, s)N_m$  where

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In differentiating w.r.t  $s$ , remember that  $t_m$  depends on  $\chi$  which, at equilibrium, must coincide with  $\psi_{\text{♂}}^*$ . Hence a differential equation for  $\psi_{\text{♂}}^*$ .

## Miracle

Everything integrates in closed form for  $Q(t)$ ,  $N_{\text{♀}}(t)$ , and for  $\psi_{\text{♂}}(q)$  all four models  $\times$  variants !

But more complicated for  $q_0 > 0$  than for  $q_0 = 0$ , because all equations are different when  $Q(t) < q_0$ .



## First model

$L_{\sigma} = q(1 - \sigma)$ , and  $q \in [q_0, q_1]$ ,  $q_0 > 0$ .

Upon differentiating  $F_{\sigma}(q, \sigma, \psi_{\sigma}^*(\sigma, \cdot))$  w.r.t.  $\sigma$  and equating to zero, we find the “first integral”:  $(1 - \psi_{\sigma}^*(q))N_m(\hat{\psi}_{\sigma}(q, \cdot)) = \text{constant}$ ,  
and  $F_{\sigma}(q, \psi_{\sigma}^*(q), \hat{\psi}_{\sigma}(q, \cdot)) = qN_m(q_0)$ .

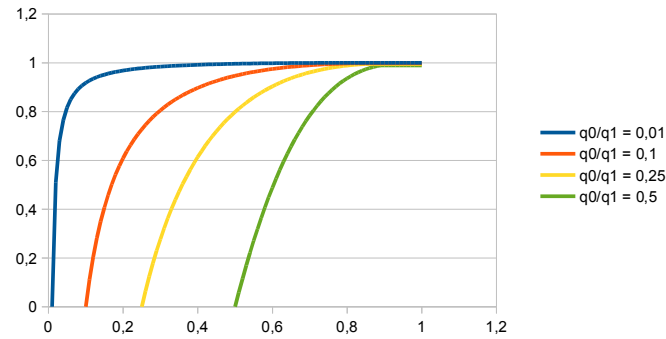
The **undesirable feature** is, for the case with variable  $\mu$  for instance,

$$\psi_{\sigma}^*(q) = \frac{(q_1 - q_0)^3 - (q_1 - q)^3}{(q_1 - q_0)^3 - \frac{q_1 - 2q_0}{q_1 + q_0}(q_1 - q)^3},$$

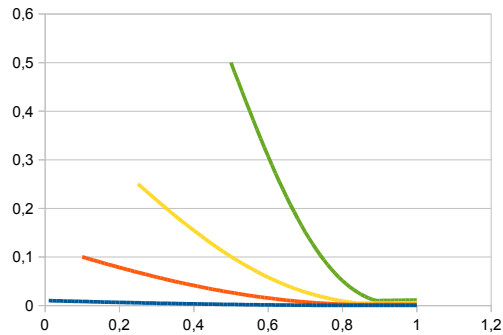
so that if  $q_0 = 0$ , it follows that for all  $q$ ,  $\psi_{\sigma}^*(q) = 1$ ,  $F_{\sigma}(q, \psi_{\sigma}^*, \psi_{\sigma}^*) = 0$ .  
(Same degeneracy appears in the other variant, with different formulas.)

# Curves for the first model (variable $\mu$ )

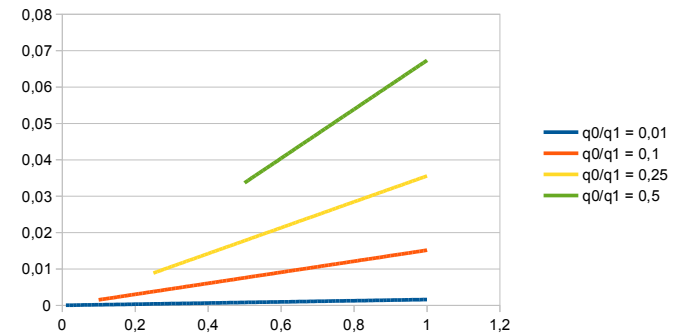
$$\lambda T = 8$$



$\psi_{\sigma}^*$  as a function of  $q/q_1$



$L_{\sigma}$  as a function of  $q/q_1$



$F_{\sigma}$  as a function of  $q/q_1$ .

## **A tentative explanation**

This same problem appears in Grafen's model. It is undesirable because one does not see why no mortality could happen just after reaching adulthood, or why the expected number of breeding seasons could not be very low for very low quality males.

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**A tentative explanation** (different from Grafen's) is as follows: in this model, as in Grafen's, males of almost zero quality have an almost zero marginal cost of signaling. So there is no reason why they would refrain from using an exceedingly large signal, forcing better quality males to use an even larger signal to distinguish themselves.

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This hypothesis will be tested with the second model where the marginal cost of signaling is always one. **We also offer a dynamic perspective:**

## A dynamic viewpoint

**Theorem** There is no possible equilibrium for this model with  $q_0 = 0$  and for any strictly increasing strategy  $\sigma = \psi_{\sigma}(q)$ ,  $\psi_{\sigma}(0) = 0$ .

**Proof** In order to allow for an infinite slope of  $\psi_{\sigma}$ , use its inverse function  $r := q/q_1 = R(\sigma)$ .

Compute  $F_{\sigma}(q, \sigma, \psi_{\sigma}^*(\sigma))$  differentiate assuming equilibrium, i.e.  $\chi = \psi_{\sigma}$ :

$$\frac{1}{M} \frac{dF_{\sigma}}{d\sigma} = \left[ (1-\sigma)R' - r(1-r)\left(1-r + \frac{r^2}{3}\right) \right] > (1-\sigma) \left[ R' - \frac{R(\sigma)}{(1-\sigma)} \right]$$

with  $M > 0$ . Since  $R(\cdot)$  is increasing, for  $\sigma < 1 - 1/e$ ,

$$\int_0^{\sigma} \left( R'(u) - \frac{R(u)}{1-u} \right) du > R(\sigma)[1 + \ln(1-\sigma)] > 0.$$

Thus in any neighborhood of 0, there are values of  $\sigma$  for which  $dF_{\sigma}/d\sigma > 0$ , or equivalently, in any neighborhood of 0, there are values of  $q$  for which it is advantageous to increase  $\sigma$ .  $\Rightarrow$  **not an equilibrium**.

## Second model (variable $\mu$ )

$$L_{\circlearrowright} = q - s, \quad q \in (0, q_1].$$

Let  $k := 2/(\lambda T)$ ,  $\tau := (T - t)/T$ ,  $\tau_m := (T - t_m)/T$ .

In that case,

$$Q(t) = q_1 \frac{T - t}{(k + 1)T - t}, \quad Q(0) = q_1/(k + 1),$$

$$\tau_m(s) = \begin{cases} k \frac{\chi^{-1}(s)}{q_1 - \chi^{-1}(s)} & \text{if } s < \chi(Q(0)), \\ T & \text{if } s \geq \chi(Q(0)). \end{cases}$$

$$N_{\circlearrowleft}(t) = N_{\circlearrowleft}(0) \left( \frac{k + \tau}{k + 1} \right)^2,$$

## Males' strategy

$$F_{\sigma^*}(q, s, \psi_{\sigma^*}^*(s)) = \frac{\mu_0 T}{(k+1)^2} (q-s) (k^2 \tau_m(s) + k \tau_m(s)^2 + \frac{1}{3} \tau_m(s)^3).$$

Differentiating  $F_{\sigma^*}(q, s, \psi_{\sigma^*}^*(s))$  and equating to zero, for  $s = \psi_{\sigma^*}^*(q)$ , (and identifying  $\chi(\cdot) = \psi_{\sigma^*}^*(\cdot)$ ), we get,

$$\psi_{\sigma^*}^{\prime} = q_1^3 \frac{q - \psi_{\sigma^*}^*(q)}{q(q_1 - q)(q_1^2 - q_1 q + \frac{q^2}{3})}, \quad \psi_{\sigma^*}^*(0) = 0,$$

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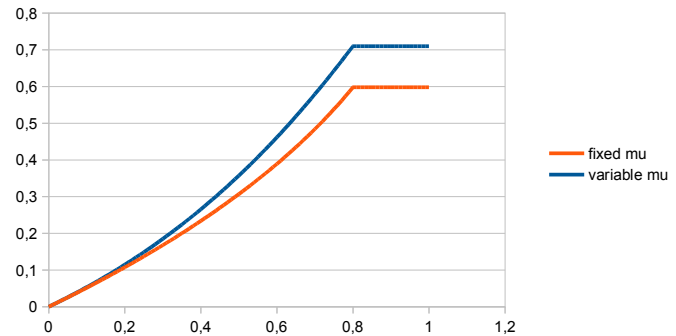
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**Miracle** This o.d.e. has a closed form solution, in terms of  $r := q/q_1$ :

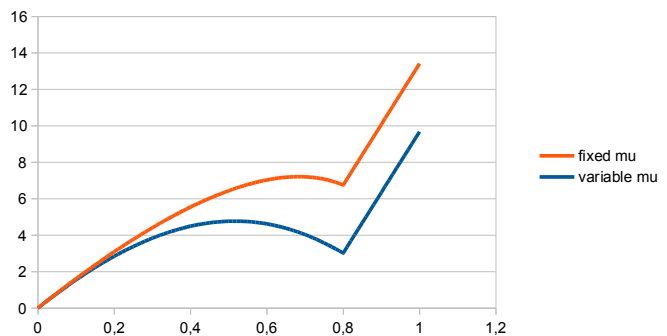
$$\Psi(q_1 r) = q_1 \frac{27r + 18r^2 + 9r^3 + 3r^4 - r^6}{2(27 + r^6)}.$$

## Curves for the second model (both variants)

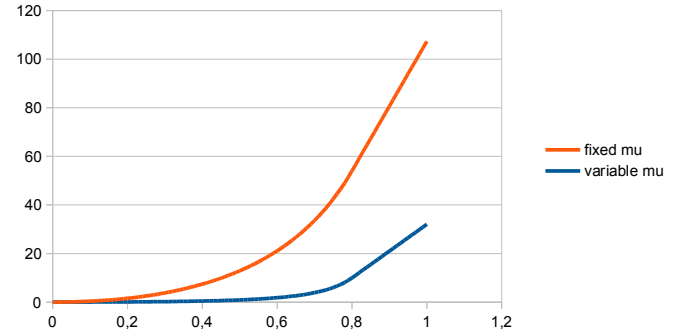
$\lambda T = 8, Q(0) = .8$



$\psi_{\sigma}^*/q_1$  as a function of  $q/q_1$



$L_{\sigma}$  as a function of  $q/q_1$



$F_{\sigma}$  as a function of  $q/q_1$

## Adaptive dynamics ♂

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$\Rightarrow$  the evolution of Males' behaviour may be studied *as if*  $\chi(\cdot) = \psi_{\sigma}(\cdot)$ .

**Hypothesis** The genes responsible for males' strategies are inherited from the father only,  $\Rightarrow$  equivalent to "clonal" reproduction.

If mutation rate independent from  $q$ , adaptive dynamics yield a PDE ( $t =$  evolutionary time,  $r = q/q_1$ ):

$$\frac{\partial \psi_{\sigma}(r, t)}{\partial t} = \frac{M}{(1-r)^3} \left[ \frac{r - \psi_{\sigma}}{(1-r)\psi'_{\sigma}} - r + r^2 - \frac{r^3}{3} \right].$$

Asymptotic behaviour ?

## Adaptive dynamics ♂

**Hypothesis** The females' behaviour is a **behavioural trait**, with an adaptation must faster than the males' **physical trait**. ( $\sim$  Ecological vs genetic.)

$\Rightarrow$  the evolution of Males' behaviour may be studied *as if*  $\chi(\cdot) = \psi_{\sigma}(\cdot)$ .

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Asymptotic behaviour ?

Work in progress ...

## What I already know

**Theorem** As  $t \rightarrow \infty$ ,

$$\begin{aligned}\psi_{\sigma^*}(0, t) &= 0, \\ \psi'_{\sigma^*}(0, t) &\rightarrow \frac{1}{2}, \\ \psi''_{\sigma^*}(0, t) &\rightarrow \frac{2}{3},\end{aligned}$$

which are their values on the signalling bayesian equilibrium.

**Proof** By examination of the characteristics of the PDE, noticeably the characteristic curve  $q(t) = \psi_{\sigma^*}(t) = 0$ ,  $\dot{\psi}'_{\sigma^*} = 2 - 1/\psi'_{\sigma^*}$ . (And some more work to get  $\dot{\psi}''_{\sigma^*} \rightarrow 4 - 6\psi''_{\sigma^*}$ .)

**Corolary** The trivial bayesian equilibrium  $\psi_{\sigma^*}(q) = 0$  is not attractive.

## What I proved after the workshop

**Theorem** Let  $0 < p_0 \leq \psi'_{\sigma}(q, 0) < 1/2$ , then if  $\psi_{\sigma}(\cdot, t)$  for  $q \in [0, Q_0]$  converges as  $t \rightarrow \infty$ , it is towards  $\Psi(\cdot)$ .

**Numerical evidence** Numerical integration of the EDP of adaptive dynamics (via the method of characteristics) shows a very precise convergence of  $\psi_{\sigma}$  towards  $\Psi$ .