# 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

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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 $m = \psi_2^\star(s)$.

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Let $s = \psi_1^\star(q)$ be, for every $q$, the strategy that maximizes $F_1(q, s, \psi_2^\star(s))$.

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

# Separating vs pooling bayesian equilibrium

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

$$\psi_2^{\star\prime}(s) = \widehat{\psi}_2'(\psi_1^{\star -1}(s)) \frac{1}{\psi_1^{\star\prime}(\psi_1^{\star -1}(s))} .$$

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

# 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.

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

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

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There is a breeding season of length $T$ each year. Let $t \in [0, T]$.

Females are all identical. They mate only once per breeding season.
Hence the number $n_{♀}(t)$ of available females decreases. $\mathbb{E}n_{♀} = N_{♀}$.
They meet males in a Poisson process of intensity $\lambda$.
They observe $s$ and decide a probability $m = \psi_{♀}(s)$ of accepting to mate.
They aim to maximize $F_{♀} = Q(0)$, the expected quality of their mate.

# Models and variants

**Two models**:

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Two variants each:

1) Males limited by their potential reproduction rate $\Rightarrow$ $\mu = constant.$

2) Males limited by the scarcity of females $\Rightarrow$ $\mu(t) = \lambda n_{\female}(t)/N_{\male}$.

## Females' behaviour

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

$$Q(t) = \mathbb{E}[\lambda \, \mathrm{d}t \, mq + (1 - \lambda \, \mathrm{d}t \, m)Q(t + \mathrm{d}t)] \,.$$

In the limit as $\mathrm{d}t \to 0$, this yields

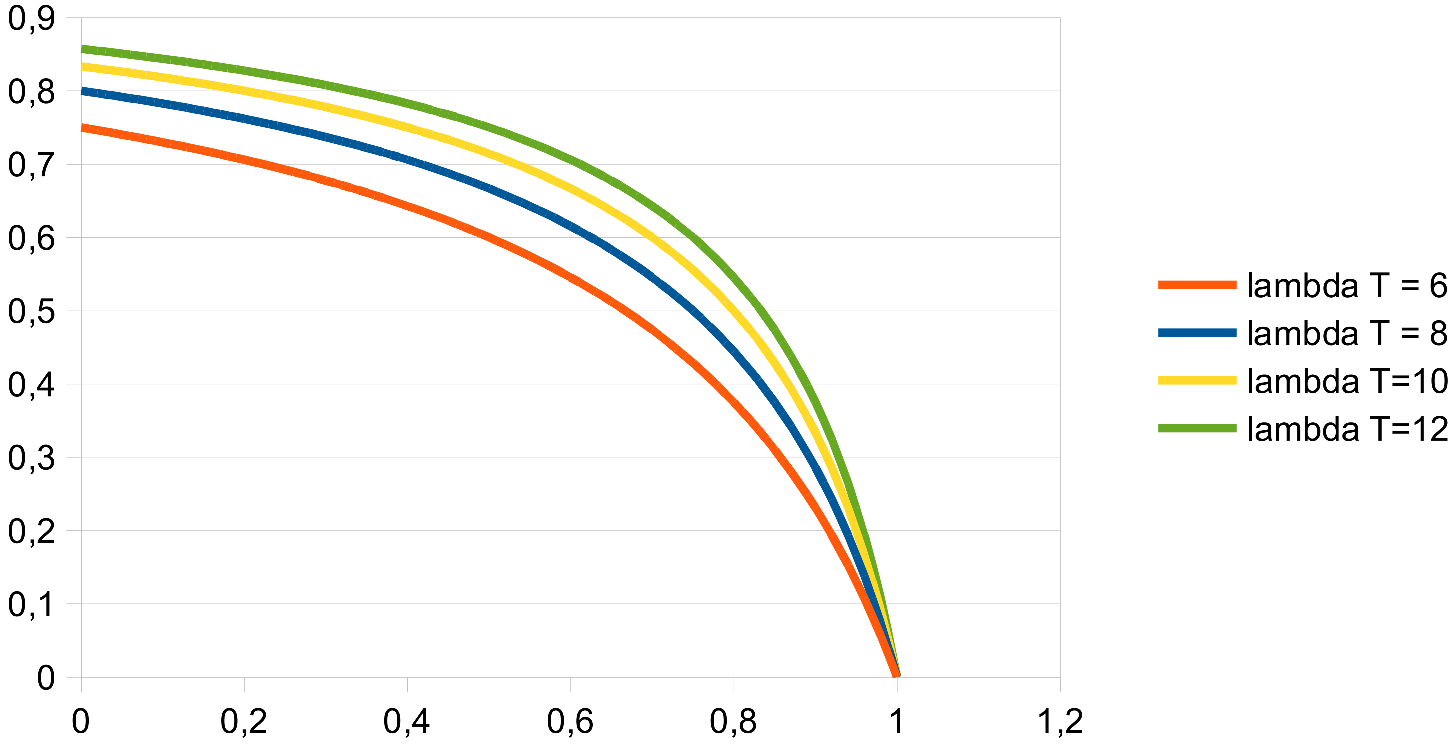
$$\frac{\mathrm{d}Q}{\mathrm{d}t} + \lambda\mathbb{E}[m(q - Q(t))] = 0 \,, \quad Q(T) = 0 \,.$$

Females' fitness $Q(0)$ maximized by

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

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. ($\sim$ Ecological vs genetic.)

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

$\Rightarrow$ Easy to show convergence, for two scenarii (function-valued trait):
Mixed strategy: $\psi_{♀}(s,t) = m \in [0,1]$.
Threshold strategy: $\psi_{♀}(s,t) = \Upsilon(s - \theta(t))$.
Both evolve toward equilibrium threshold strategy.

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Females leave the pool of available females at a rate

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Males obtain a fitness $F_{♂}(q, s, \psi^{\star}_{♀}(s, \cdot)) = L_{♂}(q, s)N_m$ where

$$N_m = \int_{t_m}^{T} \mathbb{E}\mu(t)\,\mathrm{d}t\,.$$

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

# Miracle

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

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

Upon differentiating $F_{\male}(q, \sigma, \psi^{\star}_{\female}(\sigma, \cdot))$ w.r.t. $\sigma$ and equating to zero, we find the "first integral": $(1 - \psi^{\star}_{\male}(q))N_m(\widehat{\psi}_{\female}(q, \cdot)) = constant$,
and $$F_{\male}(q, \psi^{\star}_{\male}(q), \widehat{\psi}_{\female}(q, \cdot)) = qN_m(q_0).$$

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

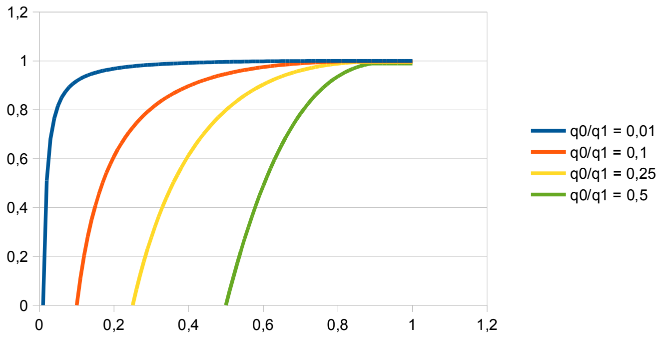
$$\psi^{\star}_{\male}(q) = \frac{(q_1 - q_0)^3 - (q_1 - q)^3}{(q_1 - q_0)^3 - \frac{q_1 - 2q_0}{q_1 + q_0}(q_1 - q)^3},$$

so that if $q_0 = 0$, it follows that for all $q$, $\psi^{\star}_{\male}(q) = 1$, $F_{\male}(q, \psi^{\star}_{\male}, \psi^{\star}_{\female}) = 0$.

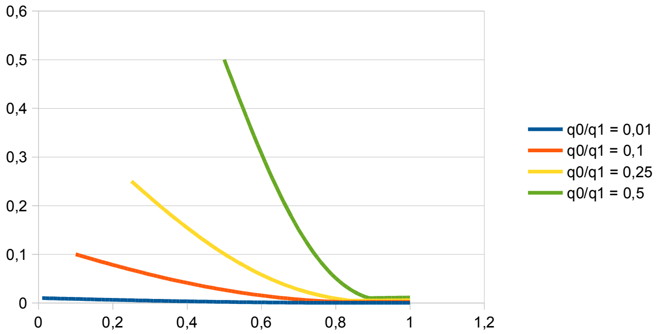
(Same degeneracy appears in the other variant, with different formulas.)

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

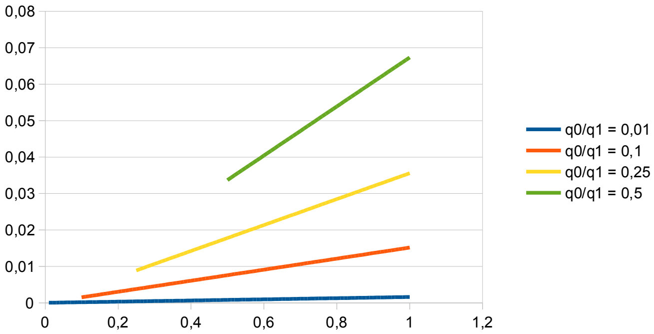
$\lambda T = 8$



$\psi^{\star}_{\male}$ as a function of $q/q_1$



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



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

# A tentative explanation

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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 $\sigma = \psi_{\male}(q)$, $\psi_{\male}(0) = 0$.

Proof In order to allow for an infinite slope of $\psi_{\male}$, use its inverse function $r := q/q_1 = R(\sigma)$.
Compute $F_{\male}(q, \sigma, \psi^{\star}_{\female}(\sigma))$ differentiate assuming equilibrium, i.e. $\chi = \psi_{\male}$:

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

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

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

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

# Second model (variable $\mu$)

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

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

In that case,

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

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

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

# Males' strategy

$$F_{\male}(q,s,\psi^\star_{\female}(s)) = \frac{\mu_0 T}{(k+1)^2}(q-s)(k^2\tau_m(s) + k\tau_m(s)^2 + \frac{1}{3}\tau_m(s)^3)\,.$$

Differentiating $F_{\male}(q,s,\psi^\star_{\female}(s))$ and equating to zero, for $s = \psi^\star_{\male}(q)$, (and identifying $\chi(\cdot) = \psi^\star_{\male}(\cdot)$), we get,

$$\psi^{\star\,\prime}_{\male} = q_1^3 \frac{q - \psi^\star_{\male}(q)}{q(q_1 - q)(q_1^2 - q_1 q + \frac{q^2}{3})}\,, \quad \psi^\star_{\male}(0) = 0\,,$$

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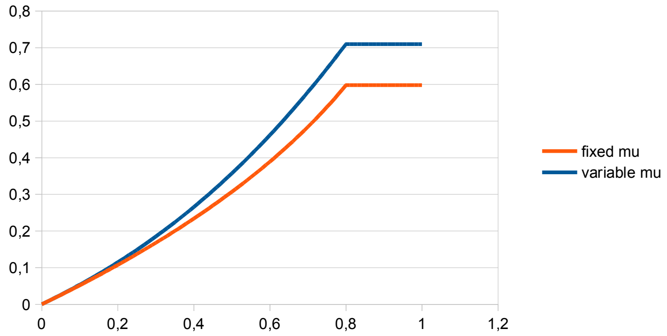
Miracle This o.d.e. has a closed form solution, in terms of $r := q/q_1$:

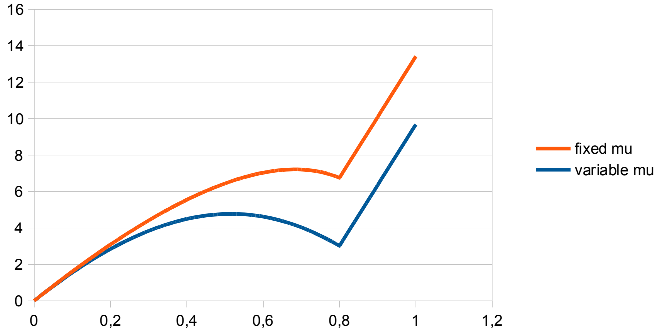
$$\Psi(q_1 r) = q_1 \frac{27r + 18r^2 + 9r^3 + 3r^4 - r^6}{2(27 + r^6)}\,.$$

# Curves for the second model (both variants)

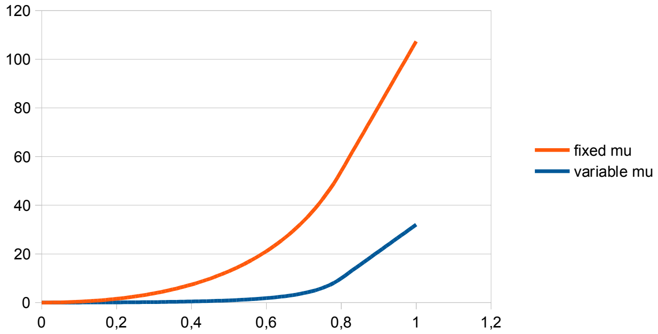
$$\lambda T = 8,\ Q(0) = .8$$



$\psi^{\star}_{\text{♂}}/q_1$ as a function of $q/q_1$



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



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

# Adaptive dynamics $\male$

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

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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, $r = q/q_1$):

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

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Asymptotic behaviour ? Work in progress . . .

# What I already know

Theorem As $t \rightarrow \infty$,

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

which are their values on the signalling bayesian equilibrium.

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

Corolary The trivial bayesian equlibrium $\psi_{\male}(q) = 0$ is not attractive.

# What I proved after the workshop

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