Evolution of preferences in structured populations: guns, genes, and culture

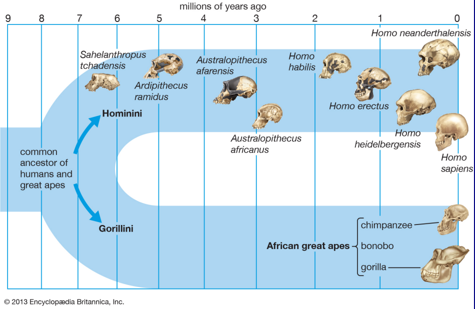
Ingela Alger, Laurent Lehmann, and Jörgen W. Weibull

Learning, Evolution, Games, Tel Aviv, June 25, 2019

$$\max_{\mathbf{x} \in F(\Omega)} \quad u(\mathbf{x})$$

Introduction

Evolution: competition between individuals for survival and reproduction



- Strategic interactions (public goods games, rent seeking, trust games, common pool resource games) must have been common
- Darwinian logic: those alive today had ancestors who were successful at surviving and reproducing; our preferences should reflect this

Introduction

Our research question

- If preferences that guide the behavior of individuals in strategic interactions are transmitted from one generation to the next, and if the realized material payoffs determine fitnesses, which preferences can evolution by natural selection be expected to lead to?

Introduction

Our research question

- If preferences that guide the behavior of individuals in strategic interactions are transmitted from one generation to the next, and if the realized material payoffs determine fitnesses, which preferences can evolution by natural selection be expected to lead to?
- Goal: understand how the *environment in which a population evolves and features of the population* affect the evolutionary viability of preferences

Introduction

Our research question

- If preferences that guide the behavior of individuals in strategic interactions are transmitted from one generation to the next, and if the realized material payoffs determine fitnesses, which preferences can evolution by natural selection be expected to lead to?
- Goal: understand how the *environment in which a population evolves and features of the population* affect the evolutionary viability of preferences
- NB: transmission can be biological or cultural

Introduction

Our research question

- Our ancestors (last 2My) lived in small groups (5-150 grown-ups), extending beyond the nuclear family (Grueter, Chapais, and Zinner, 2012, Malone, Fuentes, and White, 2012, van Schaik, 2016, Layton et al., 2012)
- Part of the environment of evolutionary adaptation of the human lineage (e.g., van Schaik, 2016)
- Impact of such group structure on evolved preferences?
- Group structure in the model: interactions within groups, some migration between groups, sometimes conflicts between groups

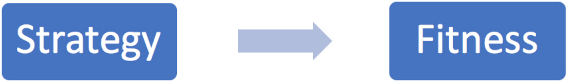
Introduction

Our research question

- Population dynamics in populations structured in groups:
  - a long-standing tradition in biology (Wright, 1931)
  - [Eshel 1972, Aoki 1982, Wilson, Pollock, and Dugatkin 1992, Taylor 1992, Taylor and Irwin 2000, Gardner and West 2006, Johnstone and Cant 2008, Lehmann, Foster, and Feldman 2008, Lion and Gandon 2010, Bao and Wild 2012, and Micheletti et al. 2017]
  - Surveys: Lehmann and Rousset (2010), Van Cleve (2015), and Dos-Santos and Peña (2017)

Introduction

Our contribution

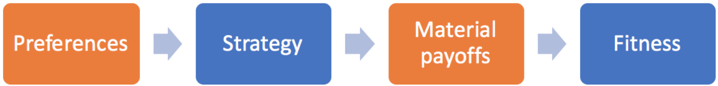


In the biology literature:

1. Results in terms of vital rates (fecundity, mortality, etc)
2. Almost exclusively on strategy evolution

Introduction

Our contribution



Our contributions:

1. Results in terms of fitness and of material payoffs
2. Allow for preferences to guide the strategy choice

Introduction

Our contribution

- We combine the island model with game theory

Introduction
Our contribution

- We combine the island model with game theory
- Lehmann, Alger, and Weibull (*Evolution* 2015): is an uninvadable strategy also a Nash equilibrium in some game between individuals?

Introduction

Our contribution

- We combine the island model with game theory
- Lehmann, Alger, and Weibull (*Evolution* 2015): is an uninvadable strategy also a Nash equilibrium in some game between individuals?
- Alger, Weibull, and Lehmann (WP 2018): uninvadable preferences

Model

Setup

- Imagine:

1. a population with an infinite number of *islands* of size n
2. evolution takes place perpetually over discrete time; each *demographic time period* consists of two phases:

- *Phase 1*: the n adults in each island play a *game*: common *strategy set* X; each individual has a preference relation on X^n, inherited from one older individual, which guides his strategy choice; resulting *material payoffs* $\pi(x_i, \mathbf{x}_{-i})$
- *Phase 2*: the realized material payoffs determine each adult's survival and fecundity; following reproduction, offspring may migrate from their native island to other islands (probability $m > 0$). After migration, individuals compete for available spots; at the end there are exactly n adults in each group.

Model

Setup

- Phase 1 and 2 together determine each adult's *individual fitness*: the expected number of her *immediate descendants* who have secured a "breeding spot" in the next demographic time period
- Fitness of i when neighbors achieve material payoffs $\boldsymbol{\pi}_{-i}$ and the material payoff in the population at large is $\bar{\pi}^*$: $w\left(\pi_i, \boldsymbol{\pi}_{-i}, \bar{\pi}^*\right)$

Model

Question

- Initially, everybody has the same preference relation, described by a utility function $u : X^n \longrightarrow \mathbb{R}$
- Suddenly exactly one individual with another utility function, $v : X^n \longrightarrow \mathbb{R}$, appears.
    - Does the resident type withstand the invasion of the mutant type?
    - How does the answer to this question depend on "first principles"?

Model

Uninvadability

- u is *uninvadable against* v if v is bound to disappear from the population in finite time (i.e., if the random number of demographic time periods during which v remains in the population is finite with probability one)
- u is *uninvadable in* Θ if it is uninvadable against all $v \in \Theta$
- To characterize the set of uninvadable utility functions, we apply a recent result in the biology literature on the stochastic evolution of traits in structured populations to preferences

Model

Uninvadability

- To this end we impose a *homogeneity assumption* concerning individual's equilibrium behavior in the subjective game:

  [H] *On all islands with the same number of mutants, and irrespective of calendar time, the same Nash equilibrium is played, and all residents use the same strategy (say, $x \in X$), and all mutants use the same strategy (say, $y \in X$).*

- Compatible with: *(i)* Θ being the set of utility functions giving rise to a unique dominant strategy; *(ii)* complete information; *(iii)* incomplete information with constant beliefs over time.
- We focus on incomplete information, and use type-homogenous Bayesian Nash Equilibria to evaluate the fitness consequences of utility functions.

Model

Uninvadability

- The set of Bayesian Nash equilibria, $B_{\mathrm{NE}}(u,v)$: the set $(\tilde{x},\tilde{y}) \in X^2$ such that $\tilde{x}$ belongs to the set of *resident strategies*

$$X_u = \left\{ \tilde{x} \in X : \tilde{x} \in \arg\max_{x \in X} \; u\left(x, \tilde{\mathbf{x}}^{(n-1)}\right) \right\}$$

and for each $\tilde{x} \in X_u$, $\tilde{y}$ is the *mutant best response*

$$\tilde{y} \in BR_v(\tilde{x}) = \arg\max_{y \in X} \; \sum_{k=0}^{n-1} p_k(\tilde{y},\tilde{x}) \cdot v\left(y, \tilde{\mathbf{y}}^{(k)}, \tilde{\mathbf{x}}^{(n-k-1)}\right)$$

Model

Uninvadability

- There may be several BNE
- Together with w and m, each BNE defines a Markov chain that induces a probability distribution over possible mutant *local lineage* realizations
- This distribution determines the average fitness of a mutant randomly sampled across all possible local lineage realizations:

$$W(y,x) = \sum_{k=0}^{n-1} p_k(y,x) \cdot \tilde{w}\left(y, \mathbf{y}^{(k)}, \mathbf{x}^{(n-1-k)}, x\right)$$

- $p_k(y,x)$: the probability for such a randomly drawn mutant that $k = 0, 1, ..., n-1$ of his neighbors are also mutants
- $W(y,x)$: the *lineage fitness* of the mutant type v given this BNE

Model

Uninvadability

- Generalization of a result due to Lehmann, Mullon, Akçay, and Van Cleve (2016):
  $u \in \Theta$ is *uninvadable* if and only if for every $v \in \Theta$,

$$W(y, x) \leq W(x, x) \;\text{ for all }\; (x, y) \in B_{\mathrm{NE}}(u, v)$$

Results

A general result

In a population $\mathcal{P} = \langle n, X, \pi, w, \Theta \rangle$, let $\hat{X}(\mathcal{P})$ be the set of uninvadable strategies:

$$\sum_{k=0}^{n-1} p_k(y, x) \cdot \tilde{w}\left(y, \mathbf{y}^{(k)}, \mathbf{x}^{(n-1-k)}, x\right) \leq 1 \quad \forall y \in X.$$

Proposition

A utility function u is uninvadable in $\mathcal{F}$ if and only if $X_u \subseteq \hat{X}(\mathcal{P})$.

Results

Utility and fitnesses

$$u_{x^*}\left(x_i,\mathbf{x}_{-i}\right)=\mathbb{E}_{\mathbf{p}\left(x_i,x^*\right)}\left[\tilde{w}\left(x_i,\tilde{\mathbf{z}}_{-i},x^*\right)\mid\left(x_i,\mathbf{x}_{-i}\right)\right]\quad\forall\left(x_i,\mathbf{x}_{-i}\right)\in X^n,$$

- $\mathbf{p}\left(x_i,x^*\right)=\left(p_0\left(x_i,x^*\right),p_1\left(x_i,x^*\right),...,p_{n-1}\left(x_i,x^*\right)\right)$: the vector of matching probabilities that would be induced if residents played x^* and mutants played x_i
- $\tilde{\mathbf{z}}_{-i}$: a *random strategy-profile* such that with probability $p_k\left(x_i,x^*\right)$ (for each $k=0,1,..,n-1$) exactly k of the $n-1$ components in $\mathbf{x}_{-i}$ are replaced by x_i, with equal probability for each such subset of k replaced components, while the remaining components in $\mathbf{x}_{-i}$ keep their original value.

Results

Utility and fitnesses

- A residential strategy under the utility function $u_{\hat{x}}$ satisfies:

$$\tilde{x} \in \arg\max_{y \in X} \sum_{k=0}^{n-1} p_k\left(y, \hat{x}\right) \cdot \tilde{w}\left(y, \mathbf{y}^{(k)}, \tilde{\mathbf{x}}^{(n-1-k)}, \hat{x}\right)$$

Results

Utility and fitnesses

- A residential strategy under the utility function $u_{\hat{x}}$ satisfies:

$$\tilde{x} \in \arg\max_{y \in X} \sum_{k=0}^{n-1} p_k\left(y, \hat{x}\right) \cdot \tilde{w}\left(y, \mathbf{y}^{(k)}, \tilde{\mathbf{x}}^{(n-1-k)}, \hat{x}\right)$$

- An uninvadable strategy $\hat{x}$ satisfies:

$$\hat{x} \in \arg\max_{y \in X} \sum_{k=0}^{n-1} p_k\left(y, \hat{x}\right) \cdot \tilde{w}\left(y, \mathbf{y}^{(k)}, \hat{\mathbf{x}}^{(n-1-k)}, \hat{x}\right).$$

Proposition

Each uninvadable strategy $\hat{x} \in \hat{X}(\mathcal{P})$ is also a residential strategy under the utility function $u_{\hat{x}}$. If it is the unique residential strategy, then $u_{\hat{x}}$ is uninvadable in $\Theta = \mathcal{F}$.

Results

Utility and fitnesses

- Kantian concern at the fitness level

$$u_{x^*}(x, y) = p_0(x, x^*) \cdot \tilde{w}(x, y, x^*) + p_1(x, x^*) \cdot \tilde{w}(x, x, x^*)$$

$$\begin{aligned} u_{x^*}(x, y, z) = p_0(x, x^*) \cdot \tilde{w}(x, y, z, x^*) &+ \frac{p_1(x, x^*)}{2} \cdot \tilde{w}(x, x, z, x^*) \\ + \frac{p_1(x, x^*)}{2} \cdot \tilde{w}(x, y, x, x^*) &+ p_2(x, x^*) \cdot \tilde{w}(x, x, x, x^*) . \end{aligned}$$

Results

Utility and material payoffs

- Interactions with marginal effects on fitnesses
- Suppose that for any $(x_i, \mathbf{x}_{-i})$ the material payoff is

$$\bar{\pi}(x_i, \mathbf{x}_{-i}) = (1-\delta)\,\pi_0 + \delta\pi(x_i, \mathbf{x}_{-i})$$

and let the fitness be

$$w(\bar{\pi}_i, \bar{\boldsymbol{\pi}}_{-i}, \bar{\pi}^*) = w\left[\bar{\pi}(x_i, \mathbf{x}_{-i}), (\bar{\pi}(x_j, \mathbf{x}_{-j}))_{j \neq i}, \bar{\pi}(x^*, \mathbf{x}^*)\right]$$

- Weak selection: consider the limit as $\delta \geq 0$ tends to 0
- Taylor expansion of fitness around δ, evaluated at $\delta = 0$: focus on first-order effects on an individual's fitness
- Key implication: $p_k(y, x) \to p_k^0 \qquad \forall x, y \in X$, $k = 0, 1, ..., n-1$

Results

Utility and material payoffs

- Let $v^0 : X^n \to \mathbb{R}$ be defined by

$$v^0(x_i, \mathbf{x}_{-i}) = \mathbb{E}_{\mathbf{p}^0}\left[\pi(x_i, \tilde{\mathbf{z}}_{-i}) - \lambda_0 \cdot \sum_{j \neq i} \pi(\tilde{z}_j,\ \tilde{\mathbf{z}}_{-j}) \mid (x_i, \mathbf{x}_{-i})\right]$$

where λ_0 is the *coefficient of fitness interdependence* under weak selection:

$$\lambda_0 = \lim_{\delta \to 0}\left(-\sum_{j \neq i} \frac{\partial w(\pi_i, \boldsymbol{\pi}_{-i}, \pi^*)}{\partial \pi_j}\right) \Big/ \left(\frac{\partial w(\pi_i, \boldsymbol{\pi}_{-i}, \pi^*)}{\partial \pi_i}\right)$$

Proposition

The utility function v^0 is uninvadable in $\Theta = \mathcal{F}$ under weak selection. A utility function $u \in \Theta$ is invadable under weak selection if $\exists \tilde{x} \in X_u$ such that $\tilde{x} \notin X_{v^0}$. Moreover, $1 - n \leq \lambda_0 \leq 1$.

Results

Utility and material payoffs

- For $n = 2$:

$$\begin{aligned} v^0(x_i, x_j) &= \left(1 - p_1^0\right) \pi\left(x_i, x_j\right) \\ &\quad - \lambda_0 p_1^0 \pi\left(x_j, x_i\right) \\ &\quad + \left(1 - \lambda_0\right) p_1^0 \pi\left(x_i, x_i\right) \end{aligned}$$

- A mix of self-interest, a Kantian concern, and a comparison with others' material payoffs

Results

Utility and material payoffs

[D] *(i)* $X = \mathbb{R}$, *(ii)* $\pi : \mathbb{R}^n \rightarrow \mathbb{R}$ *is continuously differentiable, and (iii)* $p_k : X^2 \rightarrow [0, 1]$ is differentiable for all $k \in \{0, 1, ..., n-1\}$.

Proposition

If **[D]** *holds and* $\hat{x} \in \hat{X}(\mathcal{P})$, *then*

$$[1 - \kappa(\hat{x})] \cdot \pi_1\left(\hat{x}, \hat{\mathbf{x}}^{(n-1)}\right) + \kappa(\hat{x}) \cdot \sum_{j=1}^{n} \pi_j\left(\hat{x}, \hat{\mathbf{x}}^{(n-1)}\right) = 0.$$

$\kappa(x)$ is the *coefficient of scaled relatedness*:

$$\kappa(x) = \frac{r(x,x) - \frac{1}{n-1}\lambda(x)[1 + (n-2)r(x,x)]}{1 - \lambda(x) r(x,x)}$$

Three canonical scenarios

Genes

$$
\begin{aligned}
w\left(\pi_i, \boldsymbol{\pi}_{-i}, \bar{\pi}^*\right) \;&=\; s\left(\pi_i\right) \;+\; m \cdot \left[1 - s\left(\bar{\pi}^*\right)\right] n \cdot \frac{f\left(\pi_i\right)}{nf\left(\bar{\pi}^*\right)} \\
&+\; (1-m) \cdot \left(n - \sum_{j=1}^{n} s\left(\pi_j\right)\right) \cdot \frac{f\left(\pi_i\right)}{(1-m)\sum_{j=1}^{n} f\left(\pi_j\right) + nmf\left(\bar{\pi}^*\right)}
\end{aligned}
$$

$s\left(\pi_i\right)$: probability that i survives to the next demographic time period

$f\left(\pi_i\right) > 0$: i's expected number of offspring

Three canonical scenarios

Genes

Suppose that $s(\pi_i) = s_0$ and $f(\pi_i) = f_0 \cdot \exp(\delta \cdot \pi_i)$. Then:

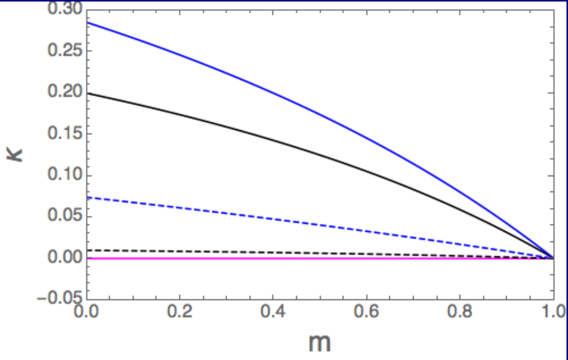
$$r_0^A = \frac{(1-m)^2 + \left(1+m^2\right)s_0}{n-(n-1)(1-m)^2 + \left(1-(n-1)m^2\right)s_0}$$

$$\lambda_0^A = \frac{(n-1)(1-m)^2}{n-(1-m)^2}$$

$$\kappa_0^A = \frac{2(1-m)s_0}{2(1-m)s_0 + n\left[2-m(1-s_0)\right]}$$

Three canonical scenarios

Genes



Black solid: $s_0 = 1/n$ and $n = 2$ Black dashed: $s_0 = 1/n$ and $n = 10$ Blue solid: $s_0 = 0.8$ and $n = 2$ Blue dashed: $s_0 = 0.8$ and $n = 10$ Pink: $s_0 = 0$

Three canonical scenarios

Guns

$$w\left(\pi_i, \boldsymbol{\pi}_{-i}, \bar{\pi}^*\right) = \left[(1-\rho) + 2\rho v\left(\boldsymbol{\pi}, \bar{\pi}^*\right)\right] \cdot \left[m \cdot \frac{f\left(\pi_i\right)}{f\left(\bar{\pi}^*\right)} + \right.$$
$$\left. (1-m)\, n \cdot \frac{f\left(\pi_i\right)}{(1-m)\sum_{j=1}^{n} f\left(\pi_j\right) + nmf\left(\bar{\pi}^*\right)}\right]$$

ρ: probability that any given island is drawn into war
$v\left(\boldsymbol{\pi}, \bar{\pi}^*\right)$: probability that an island, in which material payoff profile $\boldsymbol{\pi} \in \mathbb{R}^n$ obtains, wins a war when the average payoff in the rest of the population is $\bar{\pi}^*$

Three canonical scenarios

Guns

Suppose that $f\left(\pi_i\right) = f_0 \cdot \exp\left(\delta \cdot \pi_i\right)$ (as in the preceding example) and $v_n\left(\boldsymbol{\pi}, \bar{\pi}^*\right) = \frac{\exp(\delta \cdot n\bar{\pi})}{\exp(\delta \cdot n\bar{\pi}) + \exp(\delta \cdot n\pi^*)}$. Then:

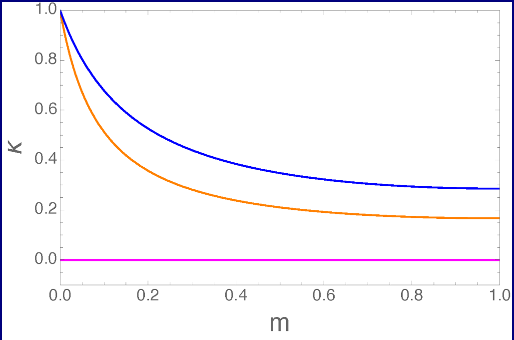
$$r_0^B = \frac{\left(1-m\right)^2}{n - \left(n-1\right)\left(1-m\right)^2}$$

$$\lambda_0^B = \frac{\left(n-1\right)\left(1-m\right)^2 - \rho\left(n-1\right)n/2}{n - \left(1-m\right)^2 + \rho n/2}$$

$$\kappa_0^B = \frac{\rho}{\rho + 2m\left(2-m\right)}$$

Three canonical scenarios

Guns



Pink: $\rho = 0$ Orange: $\rho = 0.4$ Blue: $\rho = 0.8$

Three canonical scenarios

Culture

$$w\left(\pi_i, \boldsymbol{\pi}_{-i}, \bar{\pi}^*\right) = s\left(\pi_i\right) + \; m \cdot \left[1 - s\left(\bar{\pi}^*\right)\right] \cdot \frac{f\left(\pi_i\right)}{f\left(\bar{\pi}^*\right)}$$

$$+ \; (1-m) \cdot \left(n - \sum_{j=1}^{n} s\left(\pi_j\right)\right) \cdot \frac{f\left(\pi_i\right)}{\sum_{j=1}^{n} f\left(\pi_j\right)}$$

$s\left(\pi_i\right)$: probability that i's child emulates i's trait

$(1-m) \cdot \left[n - \sum_{j=1}^{n} s\left(\pi_j\right)\right]$: expected number of children in i's island who did not emulate their parent's trait and who will emulate i's trait

$m \cdot \left[1 - s\left(\bar{\pi}^*\right)\right]$: expected number of children from other islands who did not emulate their parent's trait and who will emulate i's trait

$f\left(\pi_i\right)$: attractiveness of the trait used by i

Three canonical scenarios

Culture

Suppose that $f\left(\pi_i\right) = f_0 \cdot \exp\left(\delta \cdot \pi_i\right)$ and $s\left(\pi_i\right) = s$. Then:

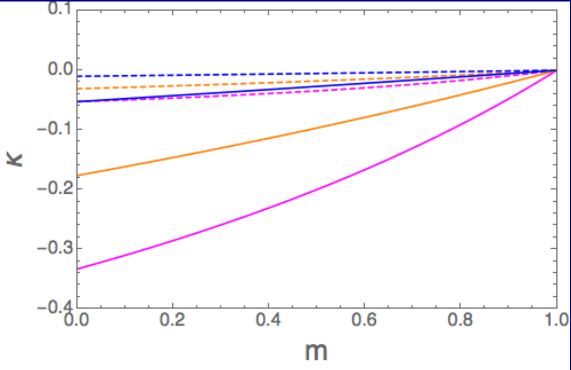
$$r_0^C = \frac{(1-m)\left[2s_0 + (1-m)(1-s_0)\right]}{n(1+s_0) - (1-m)(n-1)\left[2s_0 + (1-m)(1-s_0)\right]}$$

$$\lambda_0^C = \frac{(n-1)(1-m)}{n-(1-m)}$$

$$\kappa_0^C = -\frac{(1-m)(1-s_0)}{2n - \left[m(n-1)+1\right](1-s_0)}$$

Three canonical scenarios

Culture



Pink: $s_0 = 0$, $n = 2$ Orange: $s_0 = 0.4$, $n = 2$ Blue: $s_0 = 0.8$, $n = 2$

Pink dashed: $s_0 = 0$, $n = 10$ Orange dashed: $s_0 = 0.4$, $n = 10$

Blue dashed: $s_0 = 0.8$, $n = 10$

Concluding remarks

- Theory helps us understand how evolutionary forces may have shaped *homo sapiens*

Concluding remarks

- Theory helps us understand how evolutionary forces may have shaped *homo sapiens*
  - impact of environment on preferences

Concluding remarks

- Theory helps us understand how evolutionary forces may have shaped *homo sapiens*
  - impact of environment on preferences
  - discovery of novel preference classes

Concluding remarks

- Theory helps us understand how evolutionary forces may have shaped *homo sapiens*
  - impact of environment on preferences
  - discovery of novel preference classes
  - Alger and Weibull (*Annual Review of Economics* 2019)

Concluding remarks

- Theory helps us understand how evolutionary forces may have shaped *homo sapiens*
  - impact of environment on preferences
  - discovery of novel preference classes
  - Alger and Weibull (*Annual Review of Economics* 2019)

- Teaser: experimental study with Jörgen and Boris van Leeuwen (a WP by the end of the summer)