The Rise and Fall of Cultures

Modeling the evolution of cultural capacity, and the consequent collapse of populations

Hal Whitehead
Peter J. Richerson
• The rise of cultures
  – *Environmental Variation and the Evolution of Cultural Capacity*
  – why have some species become cultural and others not?
    Whitehead (2007) *Journal of Theoretical Biology*

• The fall of cultures
  – *The Perils of Cultural Conformism*
  – how does environmental variation and the evolution of culture put populations at risk?
    – Whitehead & Richerson (2009) *Evolution and Human Behavior*

*The role of environmental variation*
What is Culture?

• Culture is information or behaviour **shared** within a population or subpopulation which is acquired from conspecifics through some form of **social learning**
Why is culture interesting?

• The second most important form of phenotypic heritability (Maynard-Smith 1989)
  – but transmission and mutation processes and patterns different from genes
  – so cultural evolution may proceed differently from genetic evolution, e.g.
    • Inheritance of acquired variation
    • gene-culture coevolution
    • Group level adaptations
    • ….  
  – cultural species are different
Why do species differ so much in cultural capacity?

• Most species
  – no evidence of culture

• Some species
  – some evidence of one culturally-determined behaviour (e.g., some songbirds)

• A few species
  – much culturally-determined behavioural variation (e.g., chimpanzees, capuchins)

• A very few species?
  – culture a crucial determinant of behaviour and fitness (some cetaceans, elephants?)

• One species’ culture is changing the Earth
The rise of cultures

The Evolution of Cultural Capacity

• The scenario proposed by Boyd & Richerson (1985, ...) and others:
  – in the beginning genes controlled behaviour
  – selection changed population patterns of behaviour
  – but if the environment changes rapidly, phenotypic plasticity is adaptive
  – individual learning is a very effective form of phenotypic plasticity
  – but an expensive form
  – social learning (imitating, etc.) is cheaper, and now selected
  – with behaviour homogenized by social learning, we have culture
Environmental change triggers the evolution of:

- Phenotypic plasticity
- Individual learning
- Social learning
- Culture

But why in some species and not others?

Maybe differences in the perceived environment
Some suggestions

• Humans developed cultural capacity in Pleistocene as climate became much more variable (Richerson & Boyd 1988; 2004)

• Cetaceans are generally more cultural than terrestrial mammals because the ocean has more low-frequency environmental variation (Rendell & Whitehead 2001)
Pleistocene Climate Deterioration

The graph depicts the change in temperature over millions of years ago. The x-axis represents Millions of Years Ago, ranging from 0 to 6. The y-axis represents temperature, marked as δ¹⁸O, with warm and cold ranges indicated. The graph shows a trend of increasing temperatures over time. There are markers for larger-brained Homo species and smaller-brained Homo species, as well as a period marked for Australopithecines.
Later Pleistocene

Agriculture starts

Modern humans invade Eurasia

Ditlevsen et al 1996

Biologically modern humans appear

Martrat et al. 2007
Some models:

• Patterns of environmental variation should affect the evolution of different modes of behavioral control
  – Feldman et al., 1996
  – Lachmann & Jablonka, 1996
  – Laland et al., 1996
  – Wakano et al., 2004
  – Aoki et al., 2005

• Analytic models that only looked at small part of range of options
More complete model

- Individually-based, evolutionary, stochastic model
- 15 behavioural control strategies compete against one another
- Environmental variation simulated using $1/f$ noise ($\omega$ is slope of inverse power-frequency spectrum)

White Noise $\omega = 0$

Red Noise $\omega = 2$
More complete evolutionary model

- Fitness (expected number of offspring) of individual dependent on difference between its behaviour and environmental optimum

![Diagram](image-url)

- Expected offspring:
  - No offspring
  - Many offspring
  - Few offspring

- Environmental noise re. width of fitness function, $\delta$
Behavioural control strategies

• Genetic determination (G)
  – do what your genes (from parent) say + error

• Vertical social learning (V)
  – do what your parent did + error

• Horizontal social learning (H)
  – do what everyone else just did (mean) + error

• Individual learning (I)
  – do what is best in current environment + error

• 11 contingent strategies (G/V,G/H,…,G/V/H/I)
  – assess two or more basic strategies
  – do that which gives best expected return
100 model runs with:

- type of environmental noise
  - $\omega=-0.5, 0.0, 0.5, 1.0, 1.5, 2.0, 2.5$

- amount of environmental noise
  - $\delta=0.125, 0.25, 0.5, 1, 2, 4, 8$

- each set with randomly chosen
  - Survival: $\mu=\{0.75, 0.90, 0.95, 0.975, 0.99\}$/time unit
  - Behavioral accuracy: $\sigma=\{0.08, 0.15, 0.25, 0.50, 0.75\}$
  - Cost of vertical learning: $C_V=1-\{0.01, 0.03, 0.05, 0.07, 0.1\}$
  - Cost of horizontal learning: $C_H=C_V-\{0.01, 0.03, 0.05, 0.07, 0.1\}$
  - Cost of individual learning: $C_I=C_H-\{0.01, 0.03, 0.05, 0.07, 0.1\}$
  - Cost of contingency: $d=\{0.90, 0.93, 0.95, 0.97, 0.99\}$
<table>
<thead>
<tr>
<th>Time periods</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>...</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/V</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/H</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/I</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V/H</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V/I</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H/I</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/V/H</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/V/I</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/H/I</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V/H/I</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/V/H/I</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Time periods</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------</td>
<td>--------------</td>
<td>-------</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>...</td>
</tr>
<tr>
<td>G</td>
<td>100</td>
<td>97</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>100</td>
<td>103</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>100</td>
<td>88</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>100</td>
<td>95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/V</td>
<td>100</td>
<td>102</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/H</td>
<td>100</td>
<td>110</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/I</td>
<td>100</td>
<td>95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V/H</td>
<td>100</td>
<td>103</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V/I</td>
<td>100</td>
<td>96</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H/I</td>
<td>100</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/V/H</td>
<td>100</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/V/I</td>
<td>100</td>
<td>93</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/H/I</td>
<td>100</td>
<td>112</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V/H/I</td>
<td>100</td>
<td>113</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G/V/H/I</td>
<td>100</td>
<td>99</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Environment
<table>
<thead>
<tr>
<th>Time periods</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>…</th>
<th>138,645</th>
</tr>
</thead>
<tbody>
<tr>
<td>G</td>
<td>100</td>
<td>97</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>V</td>
<td>100</td>
<td>103</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>100</td>
<td>88</td>
<td>1,500</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>100</td>
<td>95</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>G/V</td>
<td>100</td>
<td>102</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>G/H</td>
<td>100</td>
<td>110</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>G/I</td>
<td>100</td>
<td>95</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>V/H</td>
<td>100</td>
<td>103</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>V/I</td>
<td>100</td>
<td>96</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>H/I</td>
<td>100</td>
<td>100</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>G/V/H</td>
<td>100</td>
<td>100</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>G/V/I</td>
<td>100</td>
<td>93</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>G/H/I</td>
<td>100</td>
<td>112</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>V/H/I</td>
<td>100</td>
<td>113</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>G/V/H/I</td>
<td>100</td>
<td>99</td>
<td>0</td>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>

The Winner!
Some technical details

• Programmed in MATLAB
• 1/f noise:
  \[ \text{ifft}\{(\text{fft}(Y)^{-\omega})\} \quad [Y \text{ is normal random variable, sd } \delta] \]
• Number of offspring:
  \[ \text{poissrnd}(w) \quad [w \text{ is vector of fitnesses}] \]
Who is left at end of 100 model runs:

- Horizontal social learners
- Individuals with contingent strategies
- Individual learners

$\omega = 1$
Represent results of runs with particular type of noise as:
So the results are:
Proportion of each strategy remaining in different environmental conditions for 100 runs
**White noise**

Noise level ($\delta$)

-0.5 0 0.5 1 1.5 2 2.5

Slope of power spectrum ($\omega$)

-0.5 0 0.5 1 1.5 2 2.5

**Red noise**

-0.5 0 0.5 1 1.5 2 2.5

Slope of power spectrum ($\omega$)

-0.5 0 0.5 1 1.5 2 2.5

---

Genetic/Individual

Vertical/Horizontal

Individual

Horizontal

Genetic

---

**Temperature: land**

-0.5 0 0.5 1 1.5 2 2.5

Slope of power spectrum ($\omega$)

-0.5 0 0.5 1 1.5 2 2.5

**Temperature: ocean**

-0.5 0 0.5 1 1.5 2 2.5

Slope of power spectrum ($\omega$)

-0.5 0 0.5 1 1.5 2 2.5

---

**Population dynamics**

-0.5 0 0.5 1 1.5 2 2.5

Slope of power spectrum ($\omega$)

-0.5 0 0.5 1 1.5 2 2.5

---

**Long-lived organisms (temp)**

**High-level carnivores**

**Short-lived organisms (temp)**

---

**Trophi level, Marine**

Inchausti & Halley 2002

Whitehead 2007
Conclusion: Evolution of Social Learning and Cultural Capacity

• Learning is more likely to evolve in long-lived animals

• Among long-lived animals, more social learning and culture
  – at higher trophic levels
  – in marine species

http://animals.timduru.org/dirlist/orca/orca-KillerWhales-15530051.jpg
The Fall of Cultures

the perils of cultural conformism

• How does culture put society at risk?
Why do societies fail?

• Competition with other societies?
• Lack of internal coherence?
• *Mismatch of human culture with environment* (Diamond 2005; Wright 2004)
A reviewer points out:

In many of these runs social learning became fixed (the only strategy left)

A problem?
Proportion of population genes vertical horizontal individual genes/vertical genes/horizontal genes/individual vertical/horizontal vertical/individual horizontal/individual genes/vertical/horizontal genes/vertical/individual genes/horizontal/individual vertical/horizontal/individual
Previous models (Boyd & Richerson 1985; Feldman et al. 1996; Wakano et al. 2004; Aoki et al. 2005) suggest equilibrium:

- Some social learners, who do better when conditions are stable
- Some individual learners, who do better when environment changes
- If all individual learners
  - social learners can invade
- If all social learners
  - no-one is tracking the environment
Previous models suggest equilibrium:

• Mixed population of social learners and individual learners, *or*

• Mixed, contingent strategy in which individuals can adopt either individual or social learning depending on the circumstances (Boyd & Richerson 1995; Henrich & Boyd 1998)
Problems during stable periods?

• Mixed population of social learners and individual learners
  – vulnerable to extirpation of individual learners?

• Mixed, contingent strategy in which individuals can adopt either individual or social social learning depending on the circumstances
  – vulnerable to invasion by pure social learners, and extirpation of mixed strategy?

“Standard” model \( \omega = 1 \)
What happens when social learners take over?

• Modify individual-based model to:
  – Just consider individual/horizontal contingent and horizontal social learners
  – Continue beyond fixation
Social learners initially do well

Approximate equilibrium

The end of individual learning!

Fitness declines

Environment is no longer tracked

Selection-induced recovery

The final collapse!

Population declines

Environment / Behaviour

Mean population behaviour

Population size

Time units
The “typical” scenario

• Social learning increases
• Contingent individuals (individual learners) are extirpated
  – especially when environment is fairly stable
• Behaviour stops tracking environment
• Fitness declines
• Population collapses and is gone

45/100 runs with standard model parameters
Collapse scenario little changed, or worsened, by:

- High individual learning costs
  - 84/100 runs collapse
- Accurate or inaccurate behaviour (amount of behavioural error)
  - 42/100, 74/100 runs collapse
- Small population size
  - 86/100 runs collapse
- More red (↑ω) or less variable (↓δ) environment
  - 82/100, 46/100 runs collapse
- Individual learning (rather than contingent), or all 15 strategies available
  - 17/100, 22/100 runs collapse
Collapse generally averted when:

- **Low individual learning costs**
  - 12/100 runs collapse

- **More variable \((\uparrow \delta)\) or less red \((\downarrow \omega)\) environment**
  - 0/100, 0/100 runs collapse
  - Horizontal learning outcompeted by individual learning in very variable or less red environments

- **Large population size**
  - 5/100 runs collapse

- **Vertical rather than horizontal social learning**
  - 0/100 runs collapse
  - Vertical social learning outcompeted by individual learning

- **Biased horizontal learning** (successful, not random, models)
  - 0/100 runs collapse
  - Biased learning allows behaviour to track environment
Collapse

• In real (red; $\omega \sim 1$) environments, during periods of stability, social learners have advantage over individual learners

• Contingent, or individual, learners may be extirpated

• Population collapse likely when society becomes completely culturally conformist
  – individuals do what everyone else does
  – environmental change is not tracked

Evolutionary changes in the behavioral strategies that individuals use to interact with their environment can precipitate population collapse
Applicability of model to humans

- Humans do not seem to have fixed, genetically-determined learning strategies (as indicated by model)
- However, learning strategies may be parentally learned (equivalent to genetics)
- And, individual humans have characteristic ways of controlling their behaviour
  - conformist, innovative, …
  - obtained from others (often parents) culturally and, perhaps, genetically
- So maybe model is a reasonable approximation for human behaviour
Real situation for human societies might be worse (1):

- Cultures can stabilize environment (food storage, irrigation, agriculture, …) for long periods, so removing advantages for individual learners
- But, culture can *cause* sudden environmental change
- Methods of stabilizing the environments of individual humans
  - heating, air-conditioning, transport, …
- simultaneously destabilizing the global environment
Real situation for human societies might be worse (2):

- learning strategy might be culturally determined (rather than genetic) increasing conformism: *a culture of conformism*
Real collapses

• Greenland Norse
  – driven to extinction (ca. 1,500AD) by cultural conformism (according to Diamond 2005)

LBK Culture
(First agriculturalists in Central & Western Europe)

Shennan 2009
Averting collapse

• Increase variability of short-term environment so individual learners have more edge
• Increase parental influence (!)
• Learn from the successful
• Encourage individual learners
  – be nice to non-conformists
Summary (1): The Rise of Culture

- Learning strategies that are likely to evolve:
  - genetic determination in short-lived, climatically-driven species
  - individual learning in long-lived, climatically-driven species
  - social learning in species whose population biology is dependent on that of other species, especially high-trophic-level marine species
Summary (2): *The Fall of Culture*

- In red environments, horizontal social learning may become ubiquitous replacing individual learning and/or contingent strategies.
- With complete conformism the environment is not tracked and the population may collapse.
- Such collapses can be averted by:
  - promotion of individual learning
  - learning from the successful
Thanks to

- Andrew Horn, Katie McAuliffe, RAM Myers, Luke Rendell, Tyler Schulz, Rob Boyd
- Reviewers (some of them!)
- NSERC, NSF