National Institute for Mathematical and Biological Synthesis (NIMBioS), Knoxville

- Mission
  - to address key biological questions by facilitating the assembly and productive collaboration of interdisciplinary teams;
  - to foster development of the critical and essential human capacity to deal with the complexities of the multi-scale systems that characterize modern biology
- Funded: National Science Foundation (biology, mathematics), US Department of Agriculture, US Department of Homeland Security
- Scientific activities
  - Working groups
  - Investigative workshops
  - Tutorials
  - Post-doctoral positions
  - Short and long-term visitors
  - More than 3,200 participants since spring 2009
- Next deadlines for requests for support: **March.1** and Sept.1
  - More info and proposal guidelines at www.nimbios.org

On the evolutionary origins of the egalitarian syndrome

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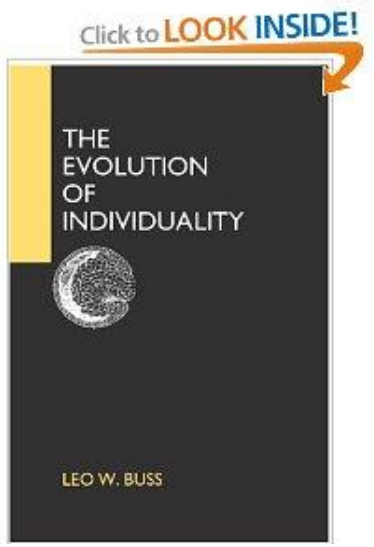
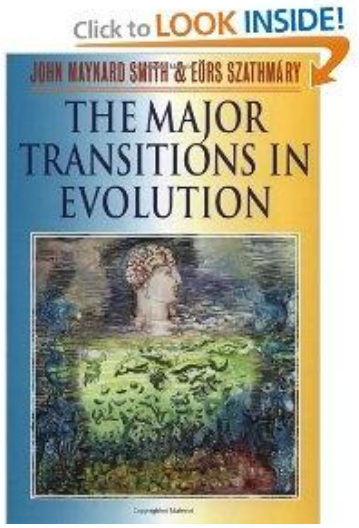
Major transitions in evolution

- Transitions in the level of biological organization
  - from independently replicating molecules to replicating molecules in compartments
  - from prokaryotic cells to eukaryotic cells
  - from asexual to sexual organisms
  - from eukaryotic cells to multicellular organisms
  - from solitary to eusocial organisms
  - from animal societies to human societies

- Dramatic growth in biological complexity and diversity





Major transitions in evolution (cont)

- In transitions in the levels of organization:
  - Groups of individuals become higher-level evolutionary individuals (units)
  - Parts of the emerging higher-level individuals/units are no longer able to live in isolation
  - Changes in the level and units of selection
  - Conflicts between lower levels and between lower and higher levels are suppressed or resolved

  - Division of labor between lower-level units.

Adam Smith on the advantages of the division of labor

- Increased dexterity from concentration of a single task,
- saving the loss of time involved in switching from one task to another, and
- the relative ease of inventing specialized machines
  - in “An Inquiry Into the Nature and Causes of the Wealth of Nations” *(1776)*

Division of labor in evolution

- the evolution of specialized enzymes with high substrate specificity from ancestors with low substrate specificity after a gene duplication,
- organelles within cells
- the evolution of specialized cell types (e.g. germ and soma),
  - Gavrilets, S. 2010. "**Rapid transition towards the division of labor via evolution of developmental plasticity**." *PLOS Computational Biology* **6**:e1000805
- limb diversification in arthropods,
- specialization of the left and right brain hemispheres in vertebrates
- the evolution of specialized (yet genetically identical) colony members in many taxa of marine invertebrates
- castes in social insects
- human societies

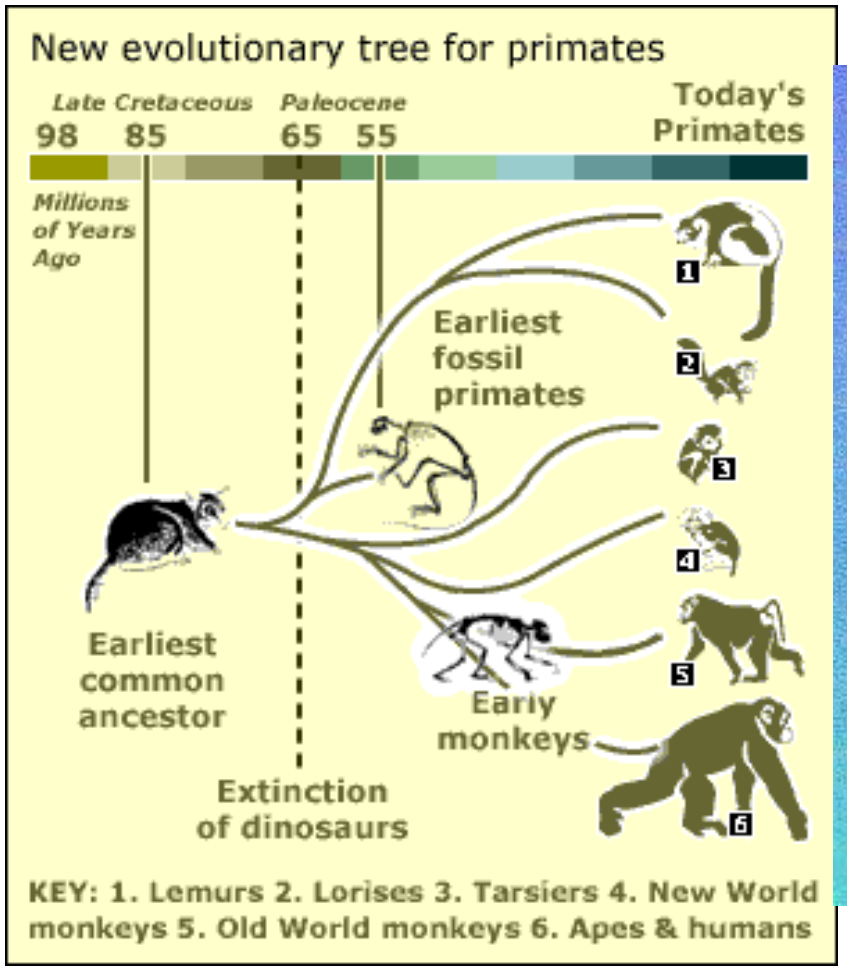
- Division of labor requires cooperation

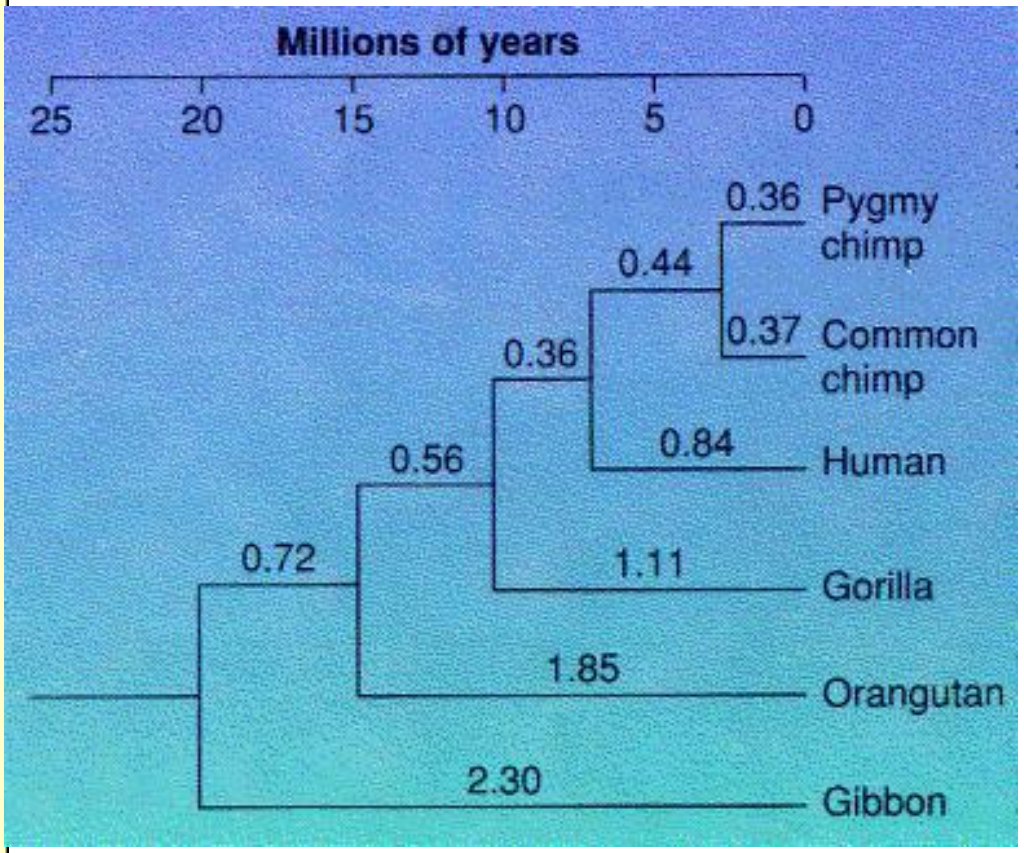
- Theory: evolving cooperation is not easy
  - Exploitation by cheaters/free-riding

- Division of labor requires cooperation

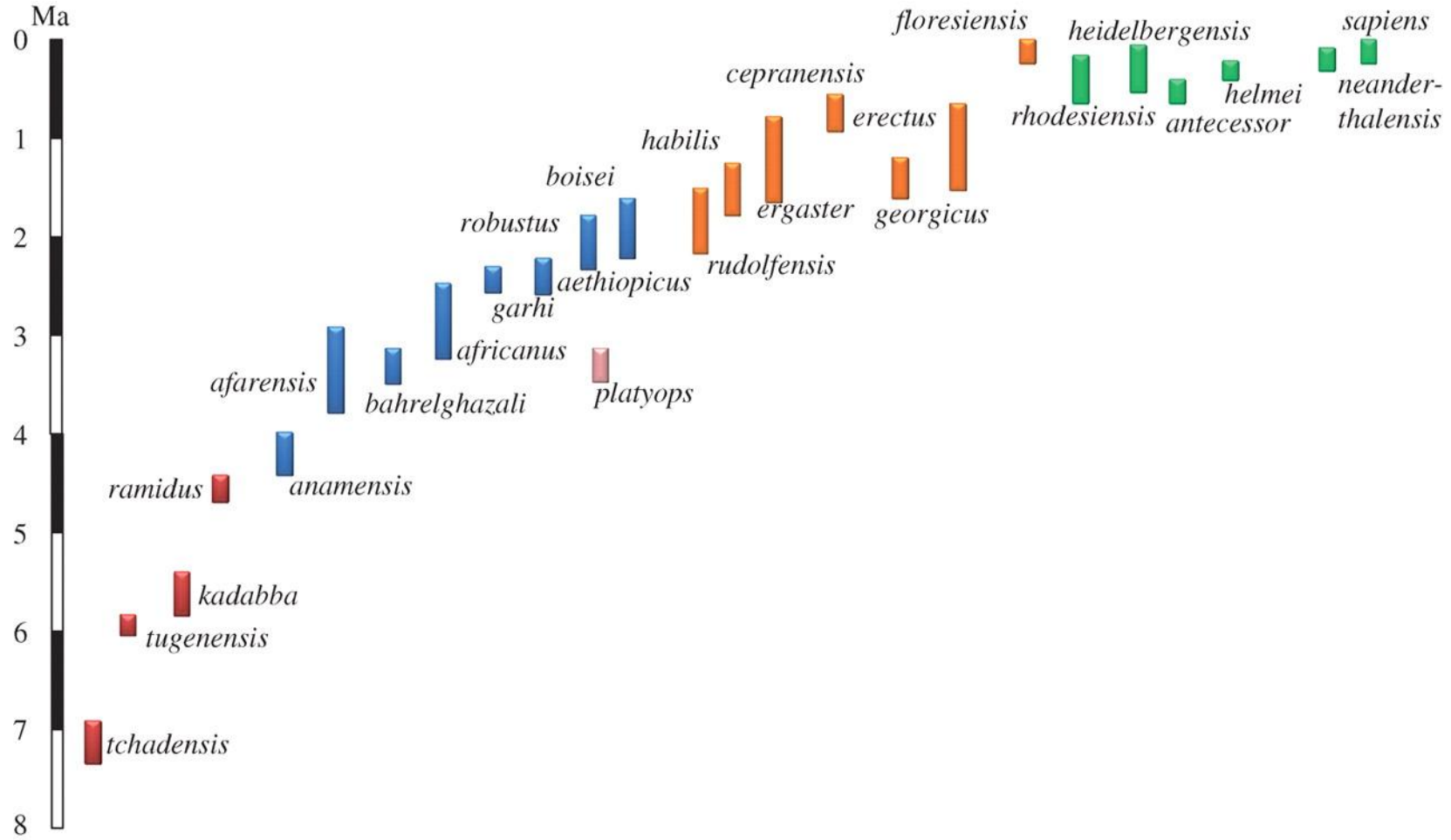
- Theory: evolving cooperation is not easy
  - Exploitation by cheaters/free-riding
  - Social structure of our ancestors (initial conditions)

Evolutionary trees for primates



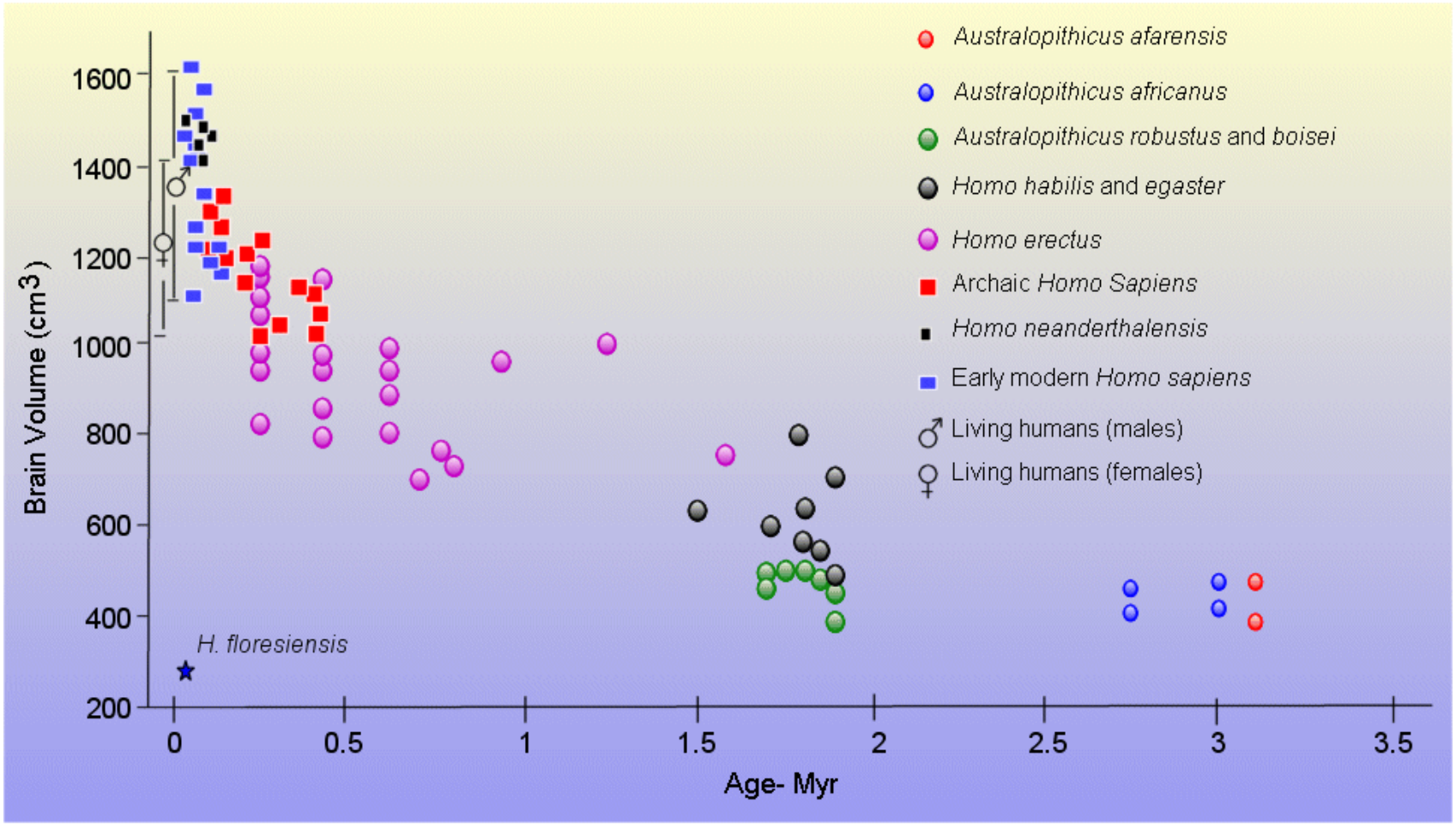


Hominin evolution.



Foley R , Gamble C Phil. Trans. R. Soc. B 2009;364:3267-3279

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B


Australopithicus afarensis
Australopithicus africanus
Australopithicus robustus and boisei
Homo habilis and egaster
Homo erectus
Archaic Homo Sapiens
Homo neanderthalensis
Early modern Homo sapiens
Living humans (males)
Living humans (females)
H. floresiensis
Brain Volume (cm3)
Age- Myr
1600
1400
1200
1000
800
600
400
200
0
0.5
1
1.5
2
2.5
3
3.5

- What makes us the “uniquely unique species”?

- How we came to be?
  - What selective forces drove the evolution of hominids?
  - What were the most important factors and mechanisms?
  - What were the relevant patterns and scales (temporal and spatial)?

- What are the implications of our evolutionary past for modern humans?

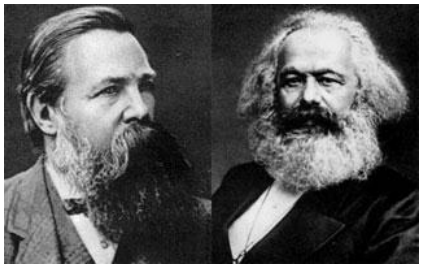
What makes us the "uniquely unique species"?

- Unusual speciation patterns (no remaining side branches)
- Rapid reduction of sexual dimorphism
- Unusual dentition
- Particular dietary niche
- Habitual bipedal locomotion
- Unusual upper limbs
- Unusual life history
- Unusual physical characteristics
- Unusual demographic and population traits
- Unusual patterns of kinship, parenting, and grand-parenting
- Extraordinary mental capabilities
- Language
- Culture
- Complex social behaviors and groups

Flinn et al. 2005

Human egalitarian syndrome

- The complex of cognitive perspectives, ethical principles, social norms, and individual and collective attitudes promoting equality
- The universality of egalitarianism in hunter-gatherers suggests that it is an ancient, evolved human pattern.
- The evolutionary emergence of this syndrome is one of the most intriguing unsolved puzzles related to the origins of modern humans.



Group-living animals

- Common interests
  - Defense from predators and acquisition and defense of various resources (including mating opportunities) from competitors which include conspecifics
- Within-group competition
  - Variation in strength/power due to a variety of reasons
  - Dominance-subordination behavior
  - Strong dominance hierarchies
    - Dominant bullies take resources (including mating) from subordinates (only weak respect for ownership in monkeys and apes)
    - Strong within-group inequality in reproductive success

Most conspicuous egalitarian features

- Meat sharing
  - Animals: tolerated scrounging; in chimpanzees, meat sometimes is traded for mating or political support
  - Foragers: widespread; hunters do not get larger shares
- Pair-bonging
  - Chimps: promiscuity and strong reproductive skew
  - Foragers: men typically have a single wife
- Political egalitarianism
  - Chimps: dominant bullies can harass any given individual or the whole group
  - Foragers: a variety of cultural practices aiming at controlling over-assertive, dominant, or highly successful individuals who might wish to monopolize resources

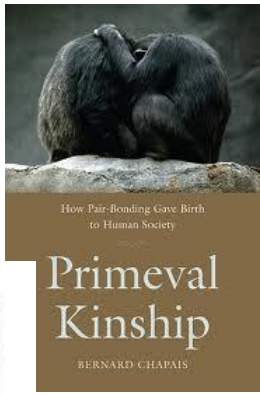
- General goal:
  - understand the evolutionary roots of and paths to human egalitarianism
  - focus on underlying social instincts which had evolved by natural selection (before the advent of culture, language, etc)

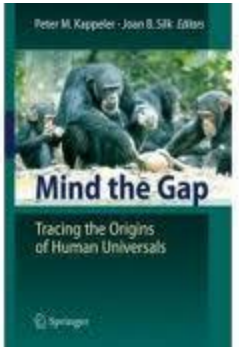
Evolutionary consequences of the transition to pair-bonding

- Major transition in life history strategy
- Pre-adaptation to paternal care and parental partnership based on the division of labor
  - Necessary to offset disproportionally high costs of raising human children
- New type of family integrating 3 generations of individuals of both sexes
- Recognition of within-group kinship networks
- Between-group kinship networks and alliances

- Hrdy, S. B. (2011) *Mothers and Others: The Evolutionary Origins of Mutual Understanding*.
- Chapais, B. (2008) *Primeval Kinship: How Pair-Bonding Gave Birth to Human Society*.
- Kappeler, P. M & Silk, J. B., eds. (2010) *Mind the gap. Tracing the origins of human universals*

- Gavrilets 2012 “Human origins and the transition from promiscuity to pair bonding” PNAS





Coalitionary control of bullies

Altruism and cooperation

- Standard theories
  - Kin selection
  - Reciprocity
  - Punishment
  - Group selection
- Their weaknesses (within the present context)
  - No social role asymmetry (bully-victim)
  - In animals, punishers are the bullies

Coalition and alliance formation theories (noncooperative)

- Focus on helping behavior, its feasibility, profitability, dynamics, and patterns
- But the number of interacting individuals is small (typically 3), no social role asymmetry
- Major approaches
  - Fitness maximization
  - From fixed behavioral rules to emergent group-level dynamics and patterns
  - Evolution of behavioral rules

Ape-state model

- A group of *N* individuals that differ in their strengths s_i
- During his lifetime, each individual discovers K resource units of value *b*

- Each time an individual (owner) takes possession of a resource unit, he is challenged by another individual (bully) who may attempt to take over the resource. Each individual can either “escalate” (i.e. fight) or “display” (i.e. do not fight).
  - Asymmetric hawk-dove game (Hammerstein 1982)

Asymmetric hawk-dove game

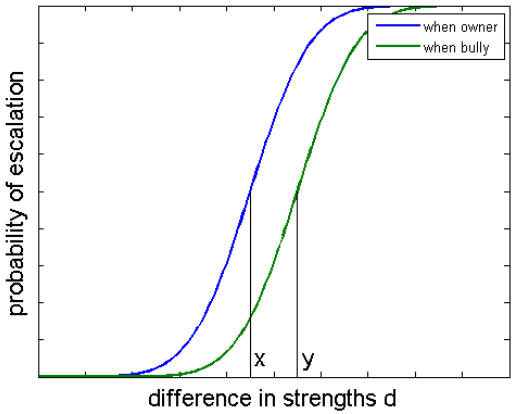
Bully

Owner		display	escalate
	display	b,0	0,b
	escalate	b,0	pb-c,(1-p)b-c

p is the probability the owner wins

Simple behavioral rule: escalate if relatively strong

- Probability of escalation ("reaction norm") is an S-shaped function of the difference in strengths $d = s_i - s_j$. Two independent genetically controlled location parameters:
  - Escalation threshold ("aggressiveness") y when bully
  - Escalation threshold ("aggressiveness") x when owner
  - The difference in strengths *d* is evaluated with an error the magnitude of which is scaled by parameter σ
  - Study the evolution of *x* and *y*
    - invasion analysis/adaptive dynamics



- Probability of winning *p* is an S-shaped function of $d = s_i - s_j$
- Winners and losers pay costs c_w and c_l, respectively
- Resource accumulated R_i controls the reproductive success:

$$w_i = \frac{R_i^{\beta}}{\sum R_j^{\beta}}$$

where β is a positive constant (Tullock contest success function)

Contest theory

- N individuals competing for a prize of value b; individual *i* makes effort x_i, pays cost cx_i
- Expected payoff $w_i = b\,\frac{x_i}{\sum x_j} - cx_i$
- More general contest success function $f_i = \frac{x_i^{\beta}}{\sum x_j^{\beta}}$

  where β is decisiveness coefficient
- Between-group contests in the presence of within-group competition
- Nash equilibria; evolutionary stable efforts x_i^*

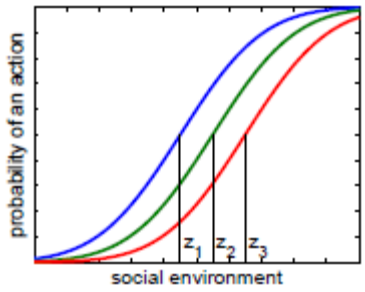
Known results for the ape-state model

- If costs of fighting are high
  - individuals evolve to become relatively cautious (i.e., they escalate only if sufficiently strong) with not much respect for ownership;
  - fights are largely avoided (weaker owners give up without fighting)
  - strong inequality in reproductive success is maintained.

- Increasing the conflict intensity (β) or the evaluation error (σ) make individuals more aggressive while increasing group size (N), or costs (c_l and c_w) have opposite effects.

Helping the victim

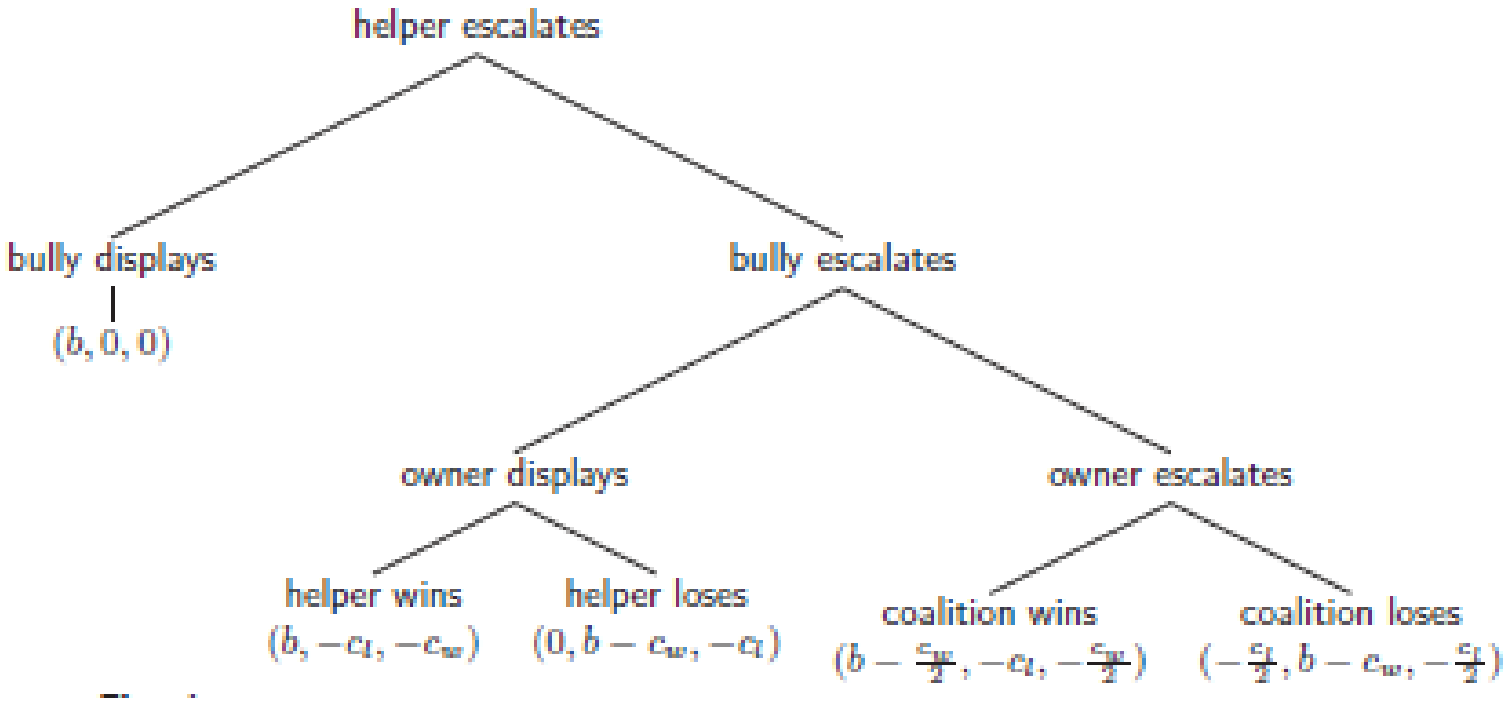
- Each owner-bully conflict is observed by a third individual who may decide to help the victim (escalate)
- Coalition strength $S = \bar{s}n^{\alpha}$, where $\bar{s}$ is the average strength of n=2 partners and α is a parameter (Lanchester-Osipov law)
- Probability of helping ("reaction norm") is an S-shaped function of the difference in strengths $d = S - s_j$; strengths are evaluated with errors
- *z* is the genetically controlled escalation threshold in the role of helper



- *x, y,* and *z* are controlled by 3 independent loci with a continuum of alleles

Helping the victim

- Payoffs to owner, bully and bystander if the bystander helps (escalates). <u>The helper's payoff is ≤0 always!</u>



Egalitarian drive

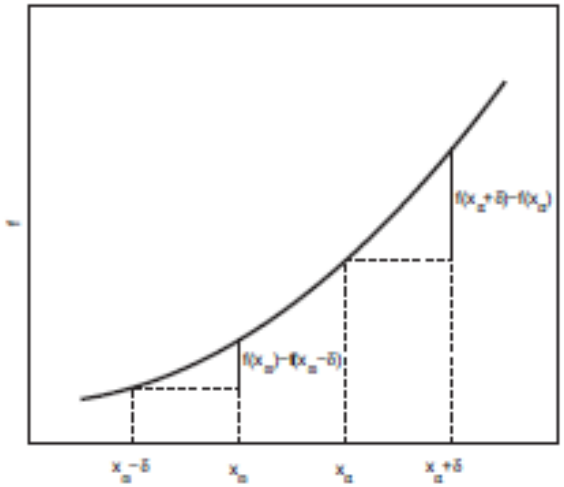
$$w_i = \frac{R_i^{\beta}}{\sum R_j^{\beta}}$$

Fitness consequences of transferring δ units from ω to α:

$$w_i = \frac{f(R_i)}{f(R_\omega)+f(R_\alpha)+\sum f}, \; w_i' = \frac{f(R_i)}{f(R_\omega-\delta)+f(R_\alpha+\delta)+\sum f}$$

Individual *i* suffers from the transfer ($w_i < w_i'$) if

$$f(R_a+\delta)-f(R_\alpha) > f(R_\omega)-f(R_\omega-\delta)$$



Always if *f(R)* grows faster than linearly!

Egalitarian drive

$$w_i = \frac{R_i^\beta}{\sum R_j^\beta}$$

- Let β=2. Then

$$\sum R_j^2 = R_i^2 + \sum_{j \neq i} R_j^2 = R_i^2 + (N-1)\overline{R^2} = R_i^2 + (N-1)[\bar{R}^2 + var(R)]$$

so that reducing variance $var(R)$ increases fitness of *i!*

- More generally, let $w_i = \frac{f(R_i)}{\sum f(R_j)}$. Then
  - If f(R) grows faster than linearly, then each individual in the group benefits if the transfer of the resource from the poor to the wealthy is prevented.
  - From one's perspective one wants to maximize the amount of the resource owned and simultaneously wants everybody else have equal amount of resource

- Q: Is this effect powerful enough to have evolutionary consequences if helping is costly?

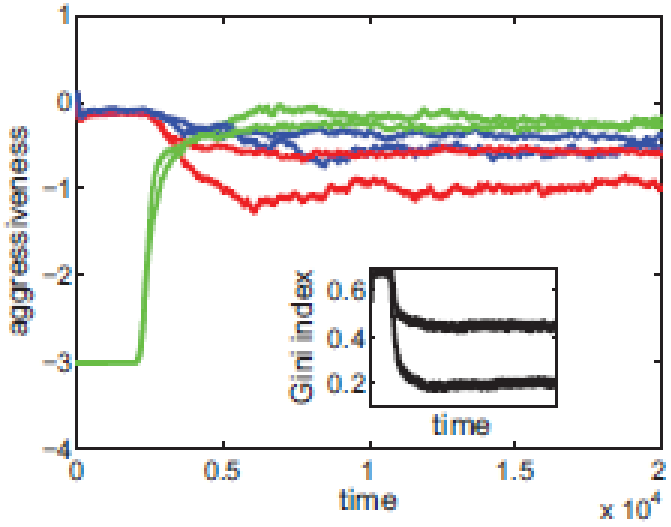
Individual-based simulations

- All possible permutations of
  - Loser cost:$c = 2,4,8$
  - Winner cost $c_w = \gamma c$ with $\gamma = 0.1, 0.2, 0.4$
  - Tullock exponent $\beta = 2,3,4$
  - St.dev. in success probability: $\sigma_v = 0.1, 0.2, 0.4$
  - St.dev. of evaluation error: $\sigma_e = 0.1, 0.2, 0.4$
  - synergicity: $\alpha = 1,2,3$

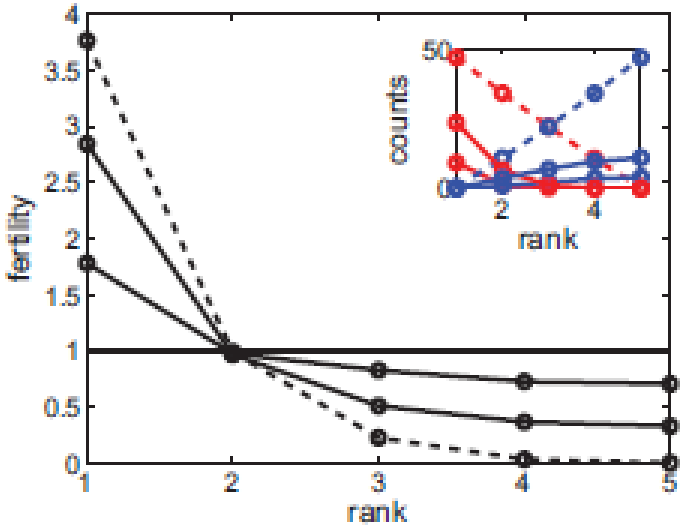
  - Fixed: group size n=10; number of groups G=200; number of encounters K=50; benefit b=1; st.dev. of strengths $\sigma_s = 1$; mutation rate $\mu = 10^{-3}$, st.dev.of mutational effects m=0.4

$\alpha = 2$ vs $\alpha = 3$

N=5

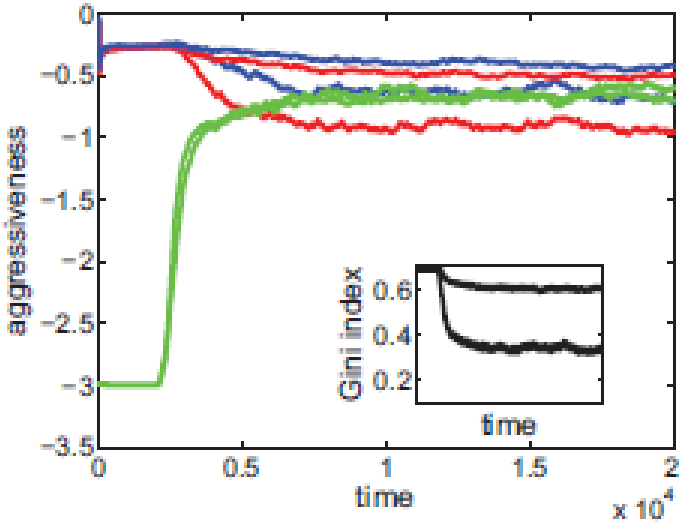


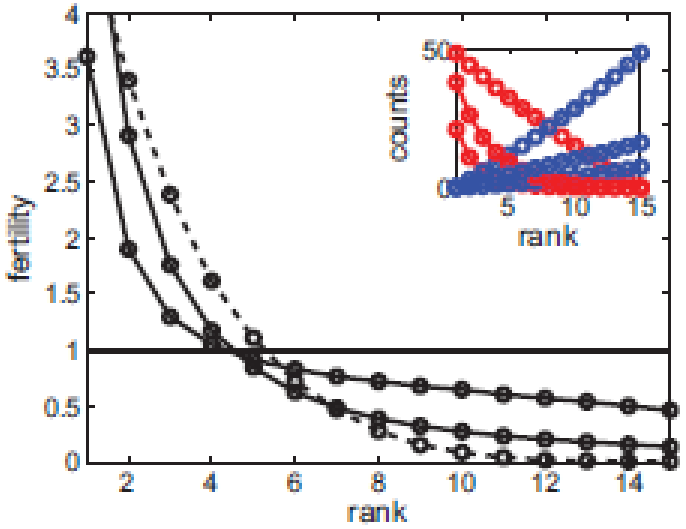
(a)



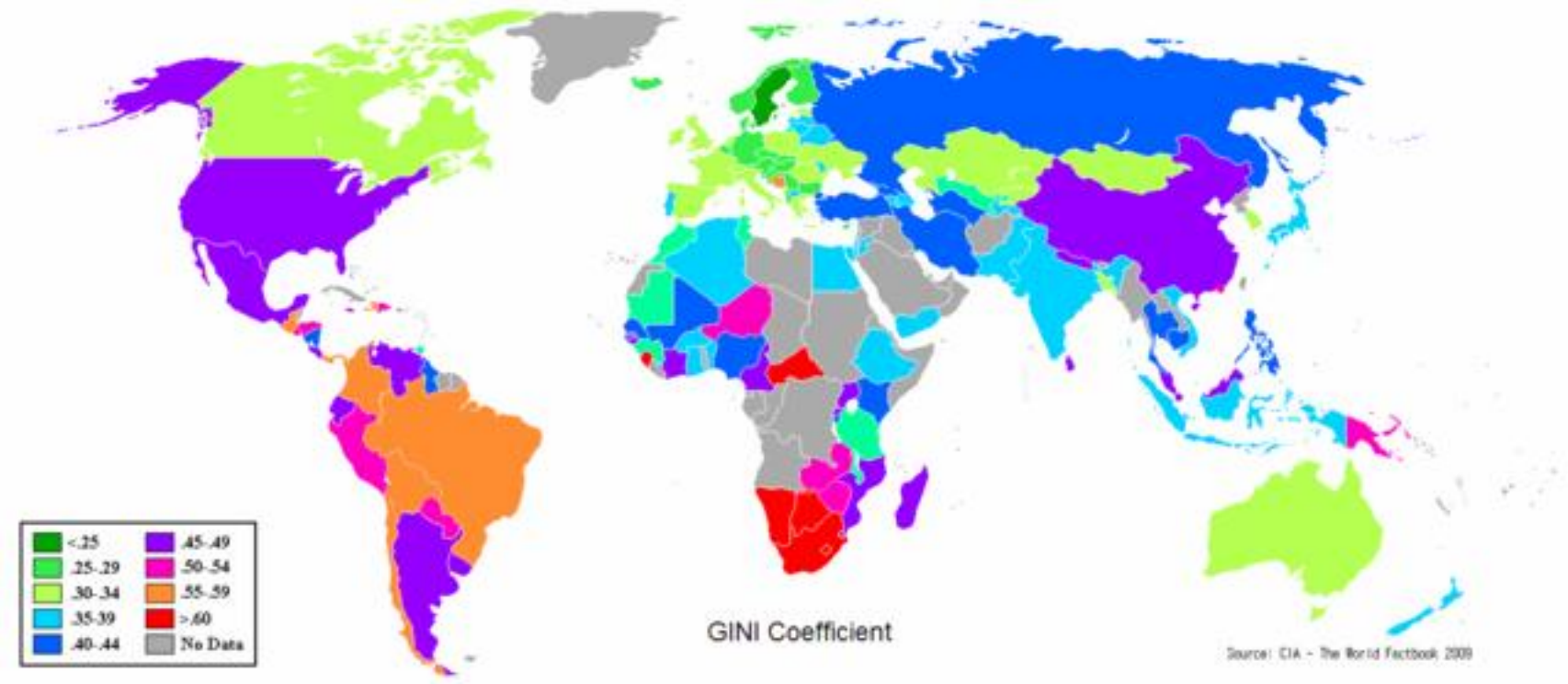
(b)

N=15

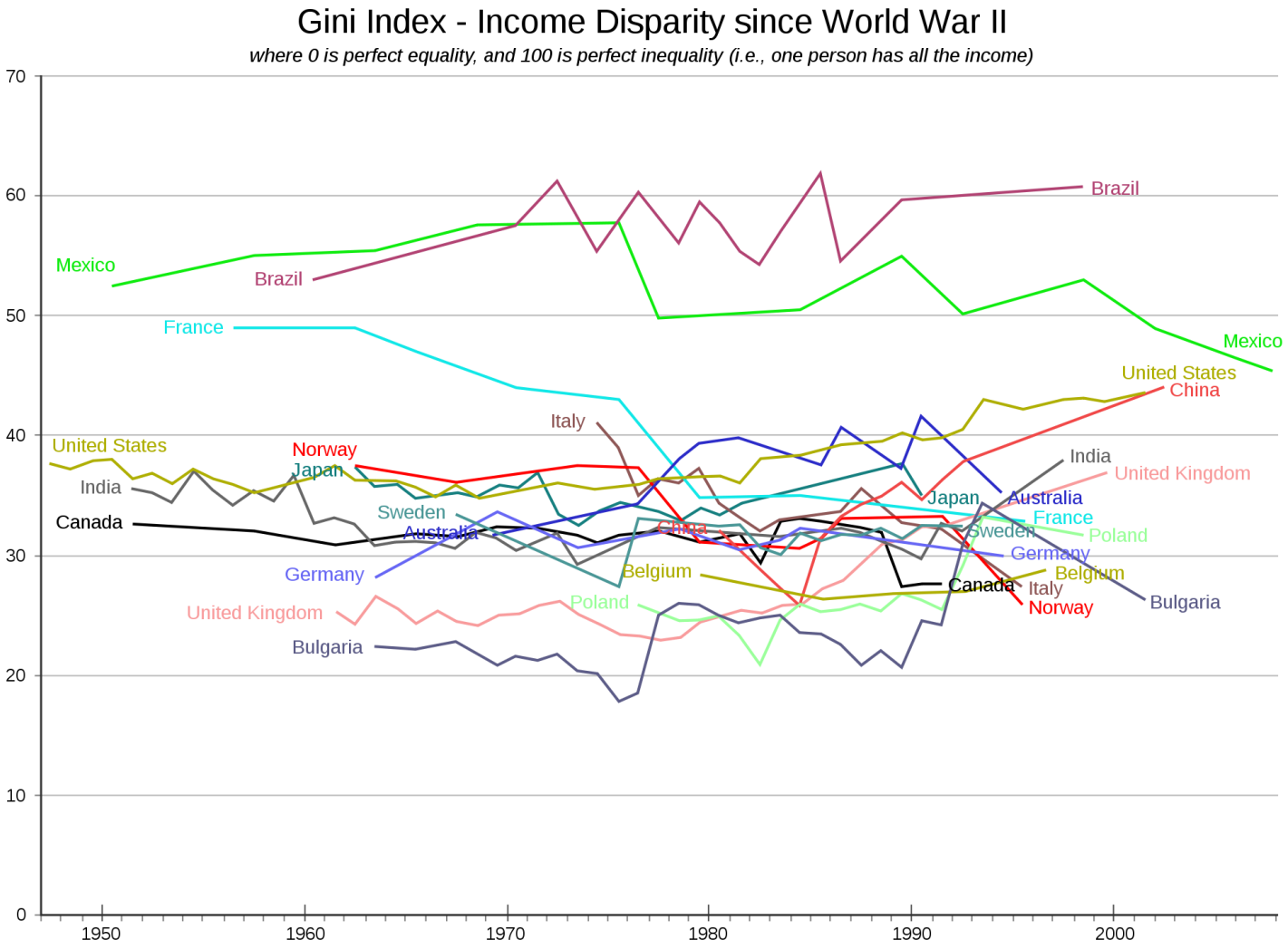




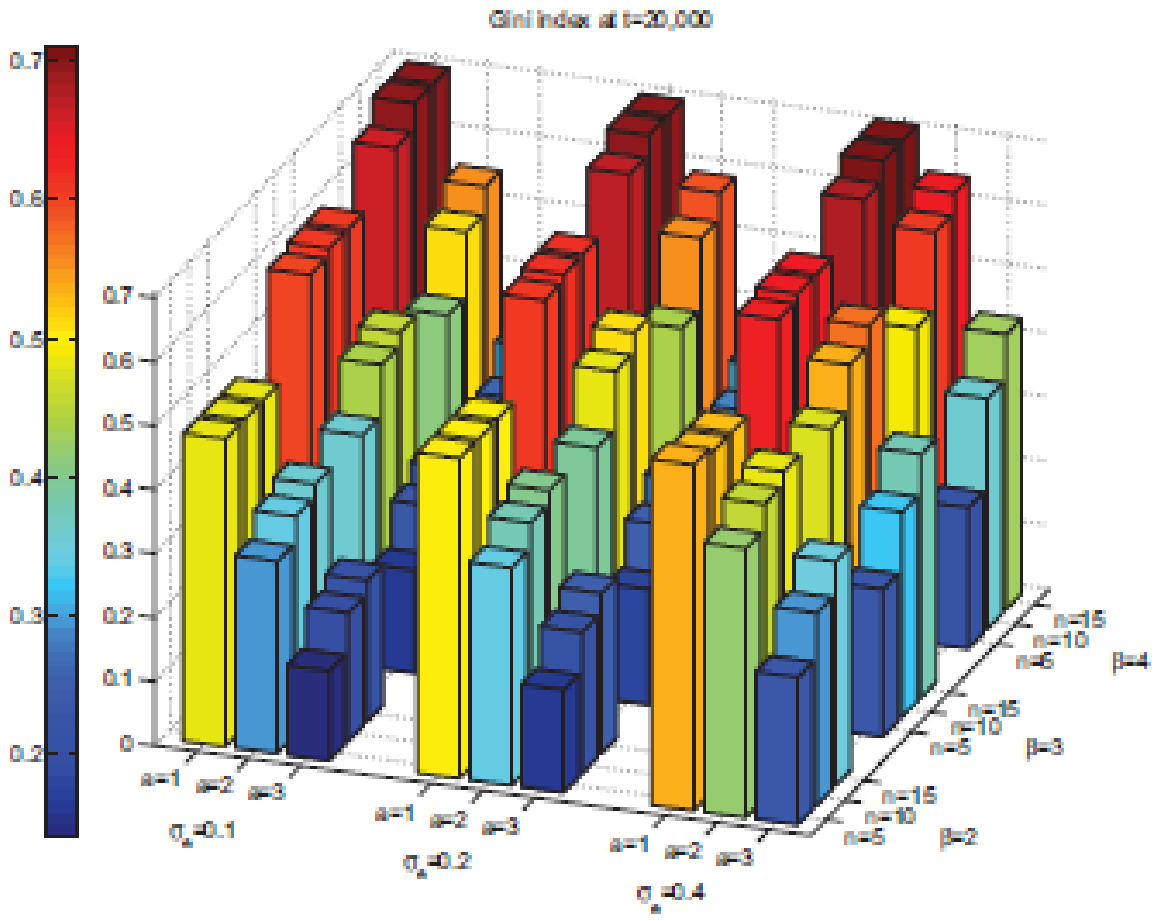
Gini coefficient



- Canada: 33, China: 47, Columbia: 59, Croatia: 29, France: 33, Russia: 40, Turkey 41, US: 41


Gini Index - Income Disparity since World War II
where 0 is perfect equality, and 100 is perfect inequality (i.e., one person has all the income)
70
60
50
40
30
20
10
0
1950
1960
1970
1980
1990
2000
Mexico
Brazil
France
United States
Norway
Japan
India
Canada
Sweden
Australia
Germany
United Kingdom
Bulgaria
Italy
China
Belgium
Poland

Effects of parameters on the Gini index of inequality in fertility (average normalized difference)



Results

- Conditions for the evolution of helping:
  - Strong synergy between strengths of coalitionary partners ($\alpha \geq 3$)
  - Stronger effect in smaller groups (smaller N) with strong pre-existing dominance hierarchies (larger β)
  - The more reliable strength evaluation (smaller σ), the more likely helping behavior

$$S = \bar{s}n^{\alpha}$$

- No complete equality and some endemic bullying persists but a dramatic decrease in the number of bullying acts
- Resulting evolutionary psychology is : “help if helping is feasible”
- Strong helping is associated with strong ownership effect

- Does not require relatedness, group selection, reciprocity or reputation

- Additional factors that would augment the effect:
  - Multiple helpers
  - Winner-loser effect
  - Differential group fertility

More general implications of the egalitarian drive

- Creates conditions for the emergence of inequity aversion, empathy, compassion, and the egalitarian moral values via the internalization of behavioral rules imposed by natural selection
- Promotes widespread cooperation via coalition formation

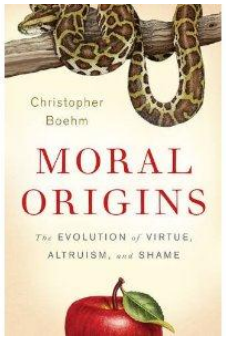
Implications for modern humans

- Instincts to dominate/bully?
- Instincts to help the weak?
- Political support for modern welfare policies?
  - Effects of physical strength?

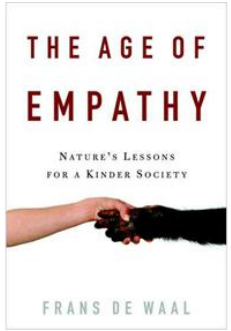
Moral values

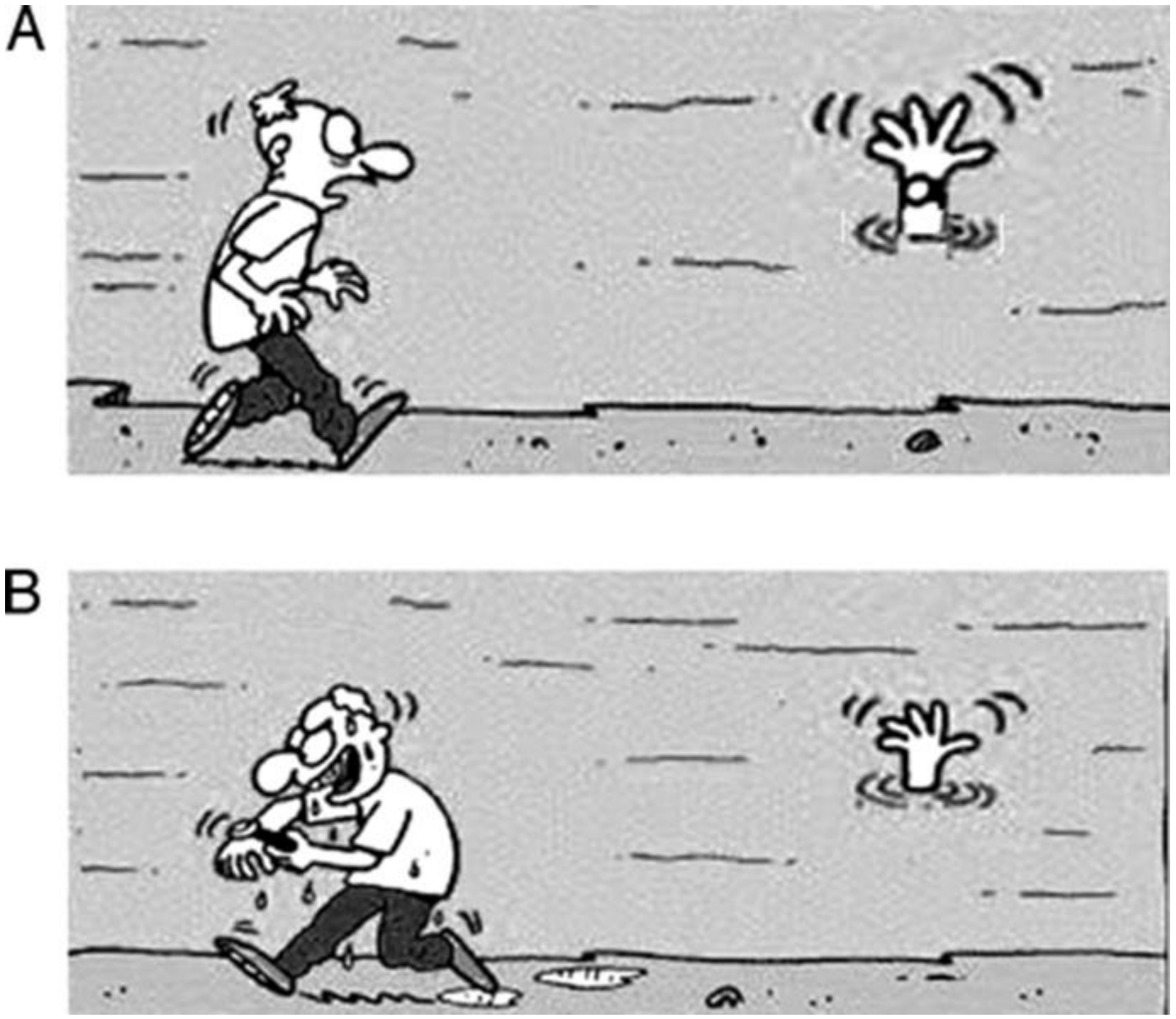
- Darwin: human morality as derived from animal "social instincts" which transform to "…moral sense or conscience as soon as … intellectual powers become … well developed"

- Chris Boehm (2012. Moral Origins: The Evolution of Virtue, Altruism, and Shame):
  - moralistic punishment, internalization of culturally enforced norms, symbolic language and gossiping, and social selection for altruism and self-restrain applied by groups to its members



- Identifying evolutionary roots for and the dynamics of genetically controlled egalitarian social instincts is a necessary step in getting a better understanding of the origins of a uniquely human sense of right and wrong.





PNAS August 2012