Collective action problem in heterogeneous groups

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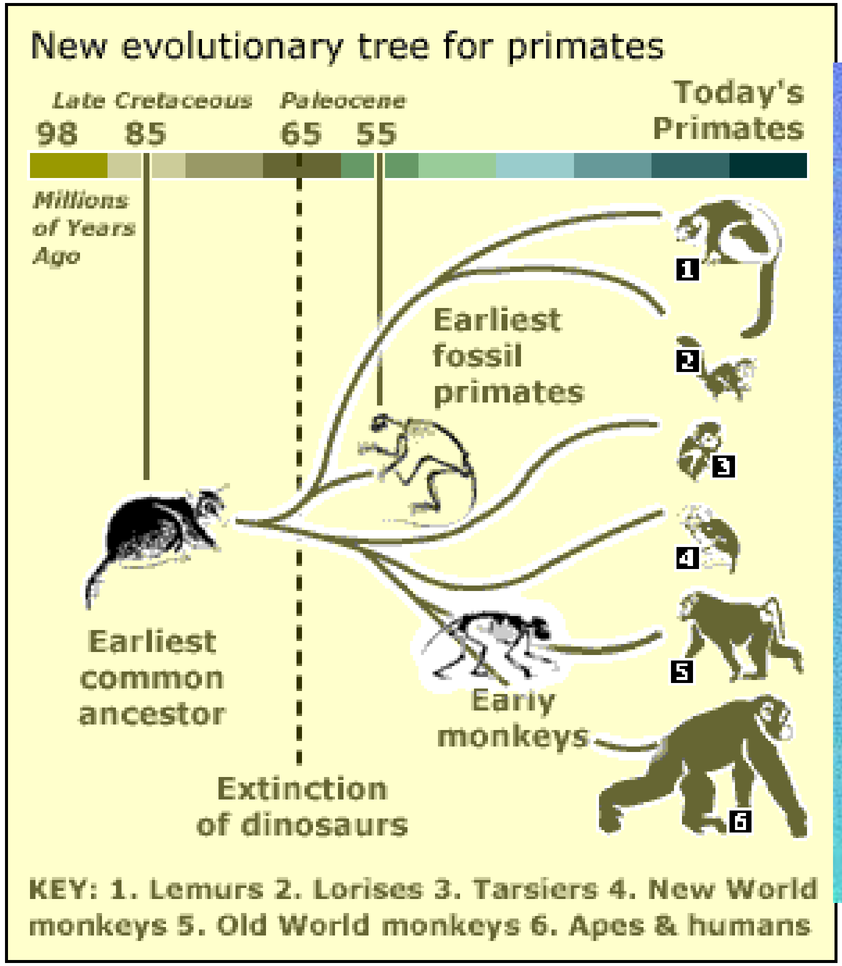
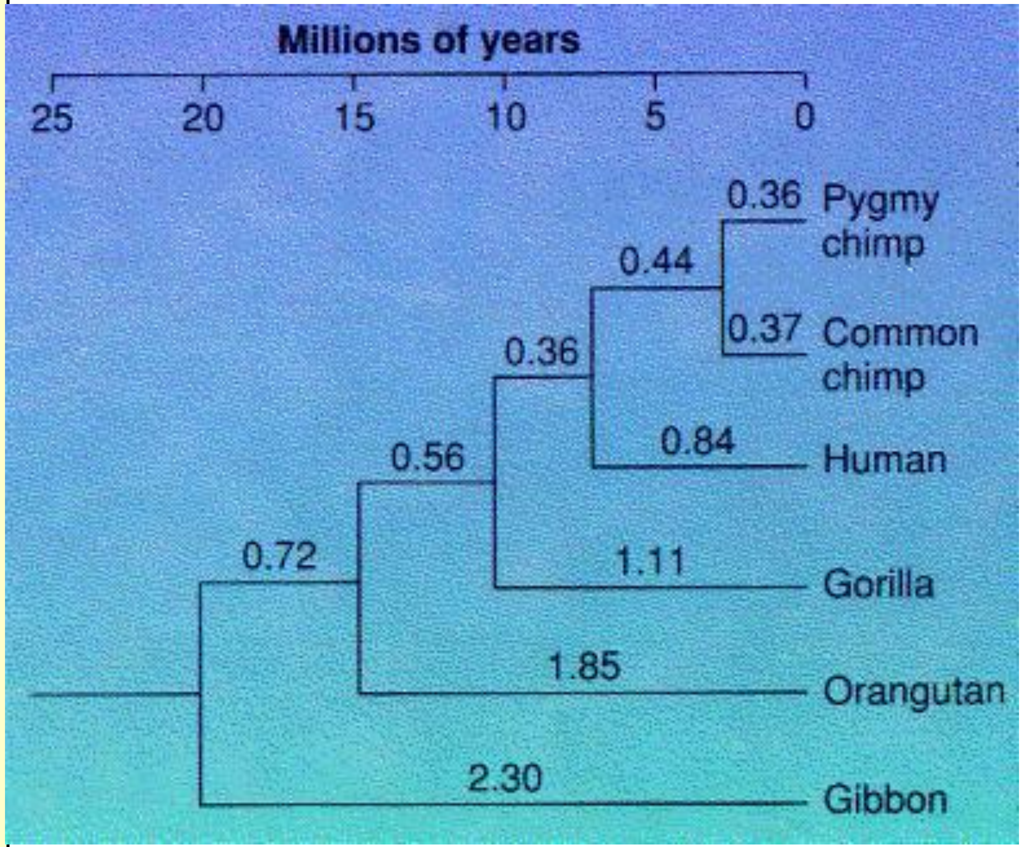
Research interests

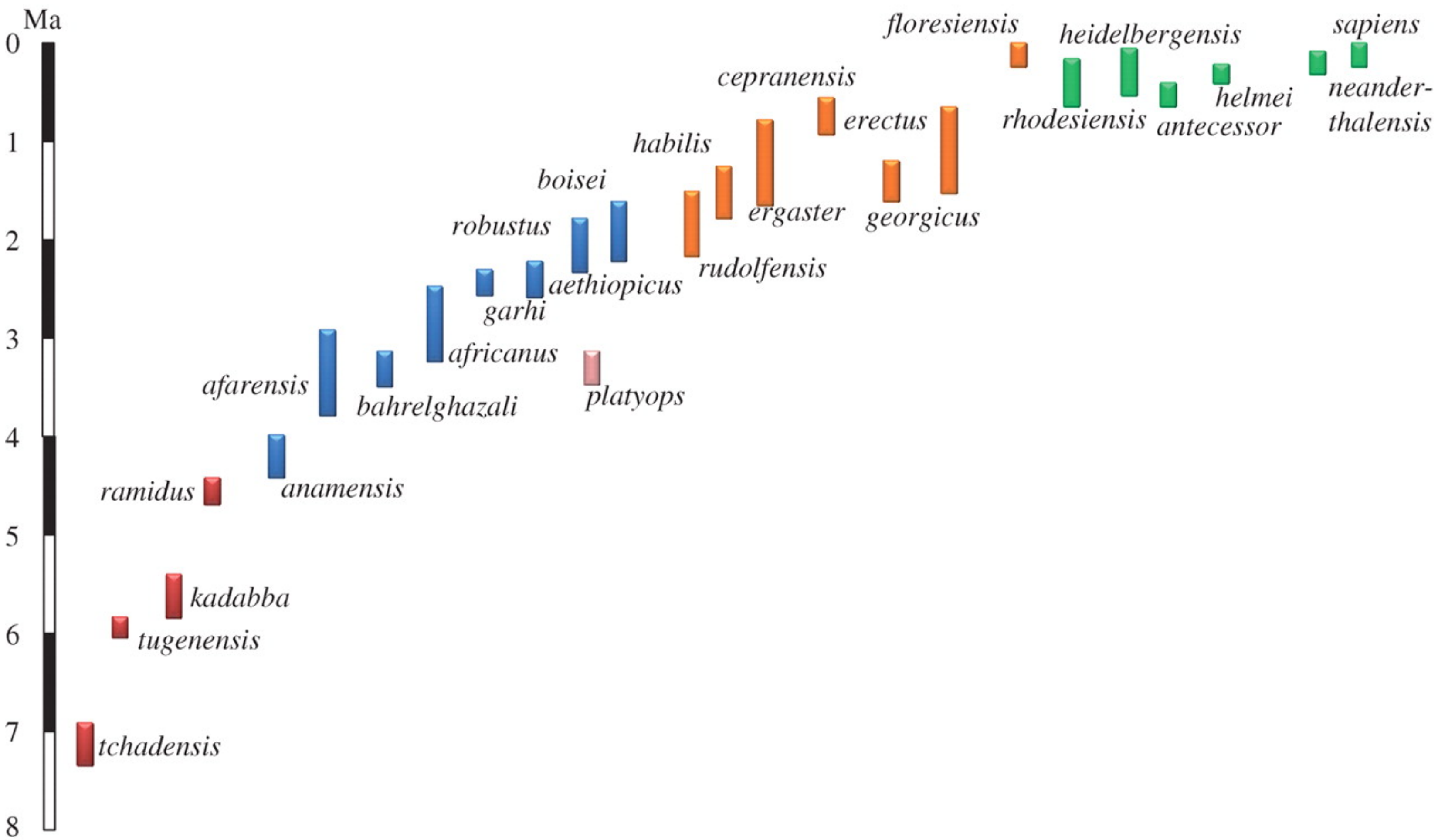
- Biological diversification:
  - speciation, adaptive radiatiation, coevolution, adaptation
- Human origins and human uniqueness
  - Mating system, cognition, coalitions, egalitarianism, hierarchy, social instincts
- Major evolutionary transitions
  - Division of labor, cooperation, multicellularity
- Human social complexity
  - Social institutions, leadership, social norms, origin and dynamics of states and empires, cliodynamics
  - Primatology, anthropology, evolutionary psychology, history, economics, military

Evolutionary trees for primates





Hominin evolution.



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

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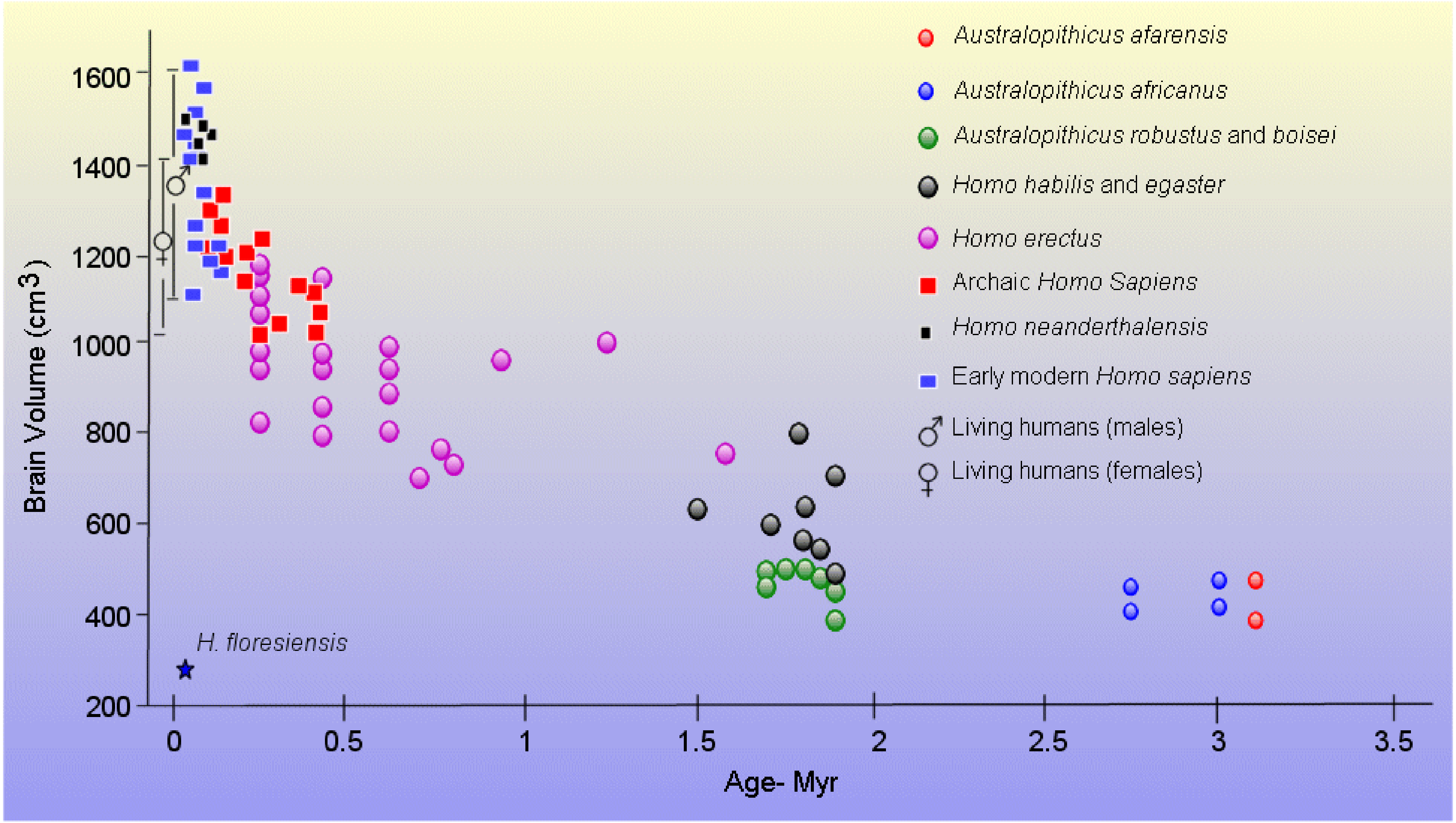
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B



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

“Big questions”

- 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

Group living

- Widespread in animals, has fitness benefits and costs, results in various adaptations for dealing with social environment

- Coordination (e.g., eating, sleeping, moving)
- Active collaboration (e.g., territorial defense, hunting, reproduction)
  - Our ancestors: large-game hunting, between-group conflicts over territories, mating and over resources

Group living

- Interdependence, collective actions, shared benefits and shared costs

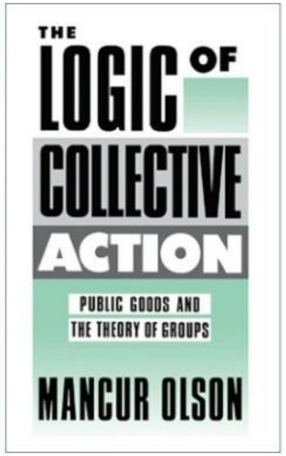
- But conflict of interests remain present
  - defection in the Prisoner’s Dilemma (Tucker 1950)
  - effort withdrawal in production of collective goods (Olson 1965)
  - over-exploitation of a communal resource (Hardin 1968)

Collective goods and free-riding

- Adam Smith’s “invisible hand” guiding the efforts of countless self-interested producers to coordinate their efforts in the interests of all
    - “By pursuing his own interest he frequently promotes that of the society more effectually than when he really intends to promote it.”

- Russell Harding (1982):
    - “… all too often we are less helped by the benevolent invisible hand than we are injured by the malevolent back of the hand; that is, in seeking private interests, we fail to secure greater collective interests”

Collective action problem (CAP)



- If a group member benefits from the action of group-mates and individual effort is costly, then there is an incentive to ‘free ride’. However, if individuals follow this logic, the public good is not produced and all group members suffer.

- Generic for situations requiring cooperation
- Overcoming it is a major challenge faced by animal and human groups

CAP in biological and anthropological literature

- Territorial conflicts in lions, wolves, dogs, many primates
- Between-group conflicts and hunting in primitive human societies
  - "limited needs" of foragers and their modest work efforts

- Hawkes (1992) and Nunn & Lewis (2006): simple two-player games to illustrate the CAP
  - But two-player models are not necessarily very informative about multi-player dynamics

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- Hawkes (1992) and Nunn & Lewis (2006): simple two-player games to illustrate the CAP
  - But two-player models are not necessarily very informative about multi-player dynamics
- Huge amount of work on cooperation

Missing factor: Within-group heterogeneity

- Ubiquitous

  - Group members differ in how much they value the collective good, how strong they are, how many resources they have, how much costs they pay per unit of effort, what their the share of the reward is, personalities, etc.

- Is inequality bad or good for collective action?
- Are large groups more or less efficient in collective action?

- Some advances in economics literature
- Not much applications to biological and anthropological problems
  - But importance is recognized in Nunn (2000) and Nunn&Lewis (2006)

Limitations of economics approaches

- Nash equilibrium vs. ESS predictions can be different
- Not much consideration of the questions of convergence to an equilibrium
- Evolutionary irrelevance of many Nash equilibria identified by game theory methods (Bowles and Gintis, 2011, Ch.5)
- Important evolutionary factors, such as genetic relatedness, spatial structure, migration, group selection, group extinction, are typically ignored

- Additional studies of biologically inspired models are needed!

- Philosophical Transactions B theme issue: *Solving the puzzle of collective action through inter-individual differences: evidence from primates and humans* (with Luke Glowaki and Chris von Rueden)

- Existing literature (both theoretical and empirical/experimental) is extremely diverse and fragmented
- Not easy to make sense of it, generalize, see common patterns

Alternative modeling approaches to CAP

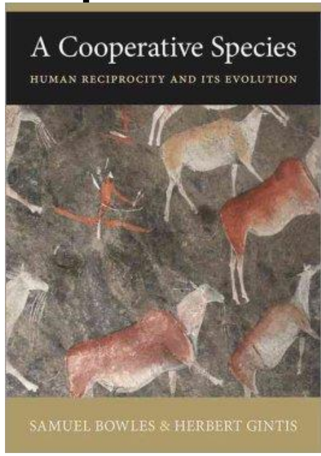
- “Collective goods” production vs. the “tragedy of the commons”
- Solution concepts: Nash equilibria, ESS, errors in decision making, effects of learning, etc.
- Types of individual “efforts”: production, competition, punishment, etc.
- Groups are formed exogenously or endogenously; coalition formation theory
- Effects of space (random interactions within groups, social networks, spatial distance)
- Decisions are made simultaneously or sequentially; “critical mass”, “bandwagon effect”, spread of contagion, role of organizers

Evolution of “social instincts” in a broad cross-specific perspective

- Genetically based propensities that govern the behavior of individuals in social interactions
  - Darwin: human morality as derived from animal “social instincts” which transform to “…moral sense or conscience as soon as … intellectual powers become … well developed”
- Evolved by natural and sexual selection
- Are plastic, resulting from interactions of the genotype with social environment
- Individual behavioral strategies are changed by random mutation (and recombination)

Generic set-up of evolutionary models

- A population comprised by a number of groups of constant size
- Individuals of 2 types: C (cooperate) and D (defect)
- Cooperators C have reduced fitness/payoff relative to their group-mates D
- Groups with a larger number of Cs win between group competition
- Limited dispersal between groups leading to an elevated within-group genetic relatedness
- Main question: can cooperation/altruism spread?



General modeling setup with heterogeneous groups

- Large number of groups of size n
- *Within-group heterogeneity (in individual shares of benefits, costs, endowments)*
- *Individual efforts/strategies are conditioned on individual "ranks"*
- *Individual efforts/strategies are treated as continuous variables*
- Group's success in producing collective goods controls the probability of group survival
- The groups that don't survive are replaced by the offspring of surviving groups
- New strategies/traits appear by mutation

Individual and group efforts

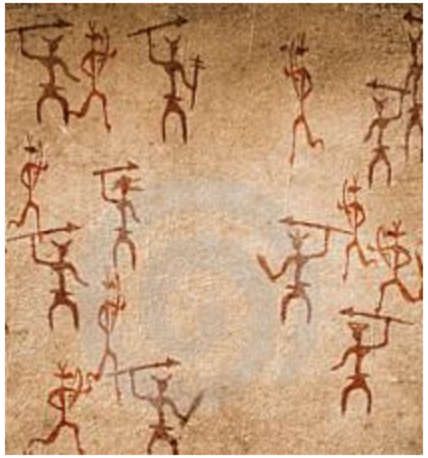
- Individual effort x_i towards the group's success in a collective action
- Group effort (impact function)

  - Additive $X = \sum x_i$
  - Non-linear $X = \left(\sum x_i^{\frac{1}{\alpha}}\right)^{\alpha}$ where α measures **collaborative ability** ("constant elasticity function" in economics literature)
    - If $\alpha \ll 1$, then $X \approx \max(x_i)$ ("strongest link)
    - If $\alpha = 1$, then additive function
    - If all $x_i = x$, then $X = n^{\alpha} x$ (Lanchester-Osipov model)

Collective actions in Pleistocene

- “Us vs. nature” games
  - Defense from predators, hunting, food collection, use of fire, etc.

- “Us vs. them” games
  - Direct competition with neighboring groups over territory and difference resources including mating



Success in collective actions

- "Us vs. nature" games: $P = \frac{X}{X+X_0}$, where X_0 is a half-success parameter
- "Us vs. them" games: $P = \frac{X}{\sum X_j}$ (Tullock contest success function)
  - Volunteer's dilemma - not Prisoner's Dilemma!
  - Nonlinear PGG and contest theory

Individual payoffs and group's survival

- Individual payoff: $$\pi_i = \pi_{0i} + bPv_i - c_i\, x_i^{\beta};$$
  - Allow for differences in
    - initial endowments (π_{0i}),
    - valuations/shares (v_i),
    - costs (c_i), and for
    - nonlinearity in costs (β)

- Group-level selection: less successful groups are replaced by offspring of more successful groups
  - Each group in this generation descends from a group from the previous generation chosen randomly with probabilities proportional to P

- Multi-level selection: group-level selection favors large values of x_i while individual level selection favors small values of x_i

Methods

- Dynamical systems & population genetic/ecology modeling
  - Invasion analysis & adaptive dynamics
  - Individual-based simulations

- Main questions: what are predicted
  - individual efforts x_i
  - group efforts X,
  - individual payoffs π_i, and
  - group production success P

General logic of evolutionary models

- Facts
  - Variation
  - Selection
  - Inheritance

- Consequence
  - Evolutionary change

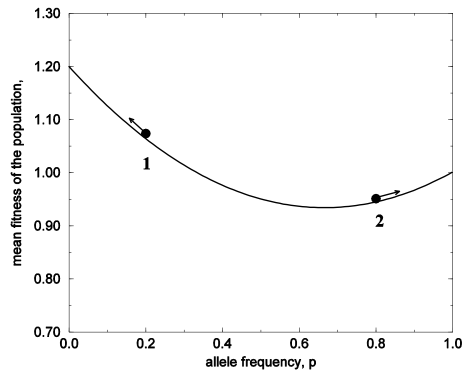
General logic of evolutionary models

- Variation
  - Discrete, continuous, mutation, recombination, random genetic drift, etc.
- Selection
  - Natural, sexual, social, habitat, etc.
- Inheritance
  - Genetic, non-genetic, gene transfer, etc.

Discrete variation

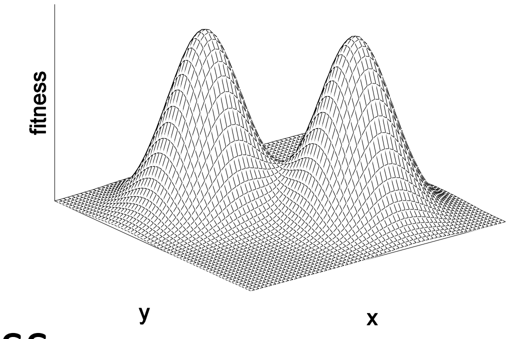
- An infinite population of asexual individuals on n types
- Frequency of type i in the current generation is p_i ($\sum p_i = 1$)
- Fitness (viability/fertility) of type i is w_i.
- Then in the next generation,
  $p_i' = \frac{w_i p_i}{\bar{w}}$, where $\bar{w} = \sum w_i p_i$ is the average fitness.
- The change per generation, $\Delta p_i = p_i' - p_i = \frac{w_i - \bar{w}}{\bar{w}} p_i$.
- If there are only two types ($n = 2, p_1 = p, p_2 = 1 - p$), then

$$\Delta p = p(1-p)\frac{d\ln(\bar{w})}{dp}$$



Continuous variation

- An infinite population of asexual individuals which differ in values x of a particular trait
- Density function $p(x)$ in the current generation.
- Fitness (viability/fertility) of trait x is $w(x)$.
- Then in the next generation,



$p(x)' = \frac{w(x)p(x)}{\bar{w}}$, where $\bar{w} = \int p(x)w(x)dx$ is the average fitness.

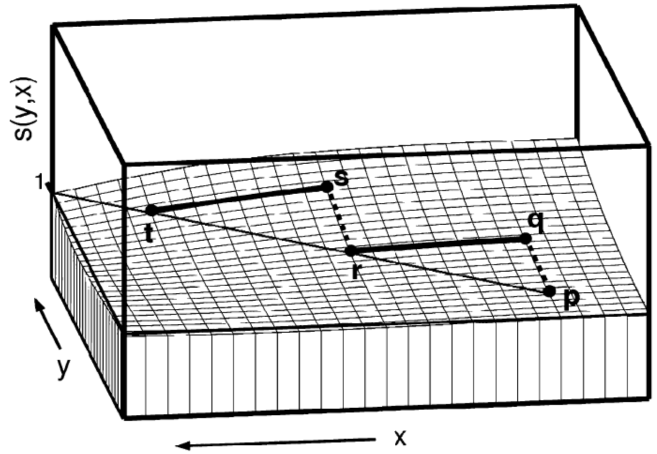
- Let $\bar{x}$ and G be the mean and variance of x in the current generation.
- Then the change per generation can be approximated (e.g. if selection is weak) as

$$\Delta\bar{x} = G\frac{d\ln(w(x))}{dx}$$

evaluated at $x = \bar{x}$

Logic of "invasion analysis"

- Individual fitness can depend on the population state, W(x,p); resulting dynamical systems have huge dimensionality and are nonlinear.
- Assume that the population is genetically (or phenotypically) uniform for trait value x except for a very small proportion of "mutants" with trait y
- Q: will mutants increase in frequency?
  - In a sense, analogous to linear stability analysis of "trivial equilibria"
- Assume that mutants that increase in frequency when rare, will replace the "resident" type. Evolutionary change as a sequence of invasion events. Invasion fitness $w(y|x)$. Fitness gradient.



Adaptive dynamics approximation

- Assumptions: rare mutations of small effects, simple genetics
- Given an invasion fitness $w(y|x)$, the change in the mean trait value is

$$\Delta x \sim D(x) = \frac{\partial w(y|x)}{\partial y},$$

where the partial derivative is evaluated at $y = x$. $D(x)$ is the "selection gradient".

Geritz et al. 1998,…., Waxman and Gavrilets (2005)

Adaptive dynamics derivations

- Rare mutant y in a population with trait x; G groups of size n
- Total mutant group effort $X = y + (n-1)x$
- Probability/extent of success in "us versus nature" games:
$$P = \frac{X}{X + X_0} = \frac{y + (n-1)x}{y + (n-1)x + X_0}$$
- Probability/extent of success in "us versus them" games:
$$P = \frac{X}{\sum X/G} = \frac{[y + (n-1)x]G}{y + (n-1)x + (G-1)nx}$$
- Invasion fitness: $w(y|x) = w_0 + bP - cy$

Adaptive dynamics derivations

- Selection gradient in “us versus nature” games:

$$D(x) = b\frac{X_0}{(nx + X_0)^2} - c$$

- Selection gradient in “us versus them” games:

$$D(x) = \frac{G-1}{G} \times \frac{b}{nx} - c$$

Results: Homogenous groups

- "Us vs nature"
  - If $b > cX_0$, each individual makes effort $x = \left(\sqrt{\frac{b}{cX_0}} - 1\right)\frac{X_0}{n}$
  - If $b < cX_0$, individuals make no effort

- "Us vs them"
  - Each individual makes effort $x = \frac{1+b}{nc}$

Gavrilets&Fortunato, 2014, Gavrilets 2015a

Important parameters for analytical derivations with heterogeneous groups

- R is a generalized benefit-to-cost parameter
- Group size n and parameters α or β measuring nonlinearity in production and cost functions
- H_q measures within-group heterogeneity where $q = \alpha$ or β
  - Generalized mean $M_q = (\frac{1}{n}\sum r_i^{\frac{1}{q}})^{\mathrm{q}}$
  - $H_q = \frac{\mathrm{M_q}}{\mathrm{M_1}}$

Results: heterogeneous groups

- Basic “us versus nature” model:
  - Benefit-to-cost ratio $r_i = \frac{b_i}{c_i X_0}$; ranked $r_1 > r_2 > \cdots > r_n$.
  - Normalized group effort $Z = \frac{X}{X_0}$
  - If $r_1 > 1$, then only rank-1 individual contributes; $Z = \sqrt{r_1} - 1$.
    - “Exploitation of the great by the small” (Olson 1965)

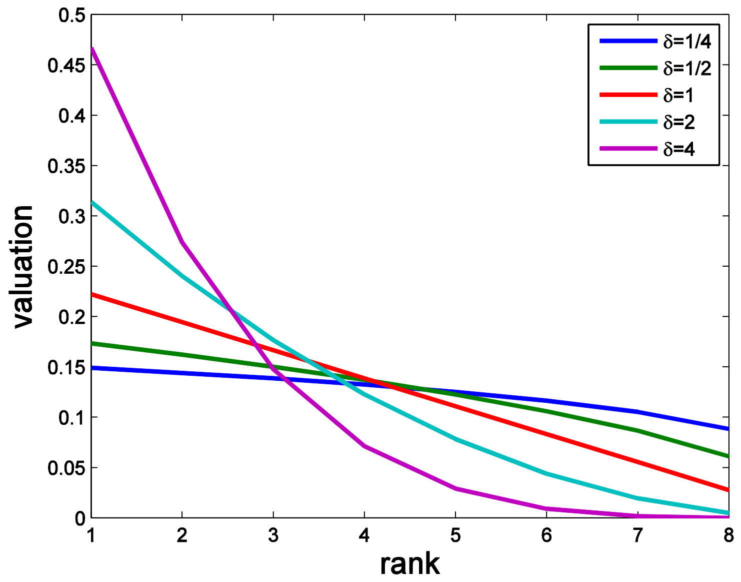
Example: heterogeneity in valuations v_i

- Group members are ranked from 1 to n

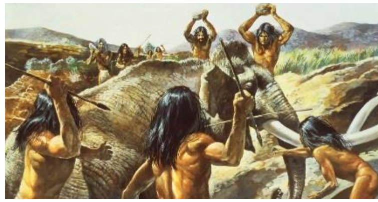
- Valuation at rank i:

$$v_i \sim (n+1-i)^{\delta},$$

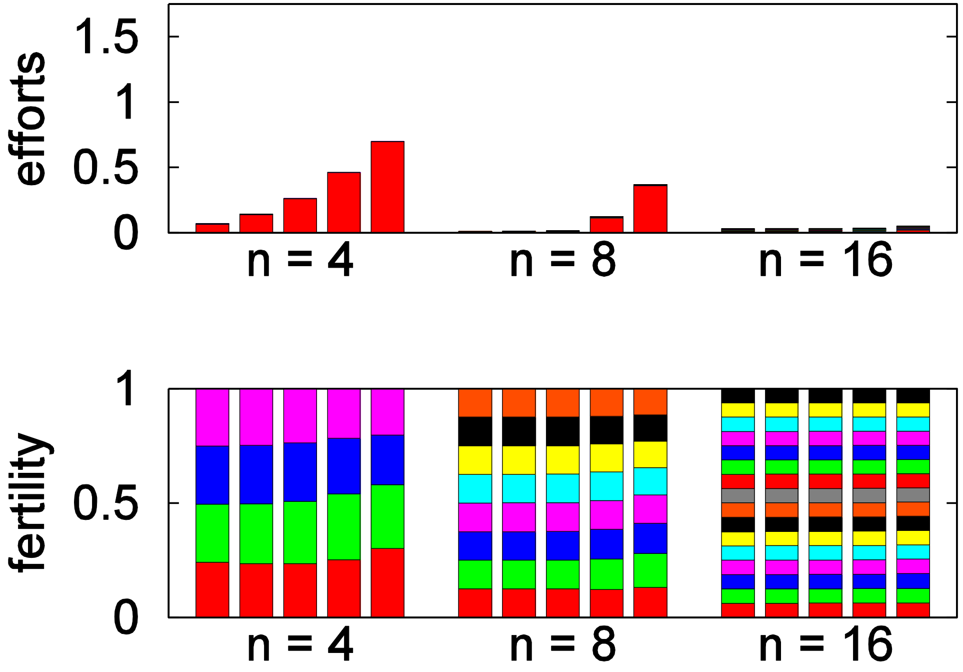
- Parameter δ measures the degree of inequality:
  - δ=0 (complete equality);
  - δ=1 (linear decay in v_i with i);
  - $\delta = 4$ (larger inequality).



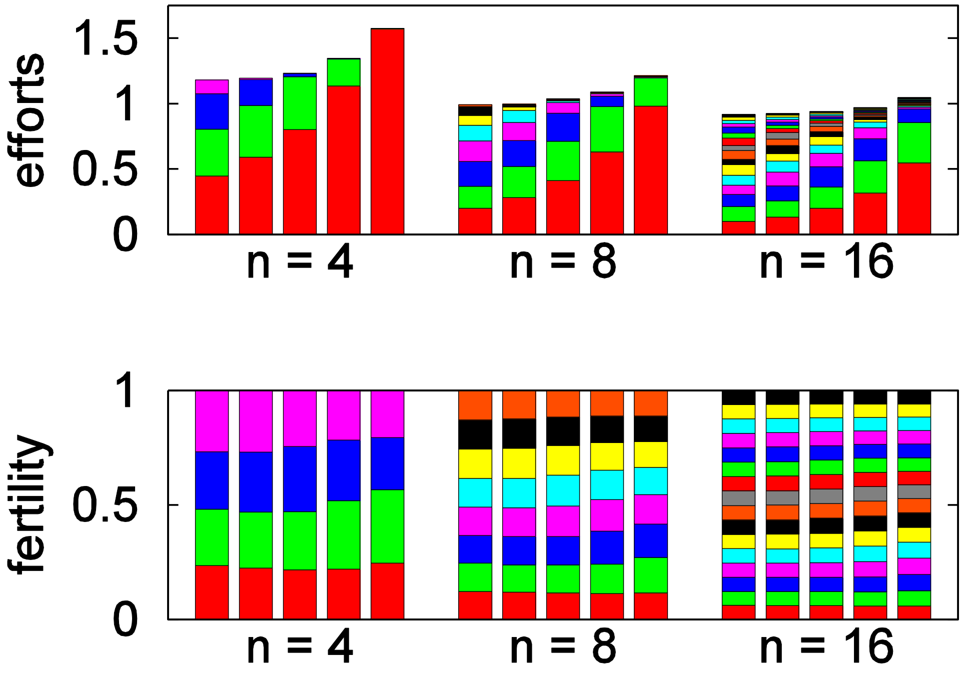
“Us vs. nature” games: linear impact and cost functions



No group extinction



With group extinction

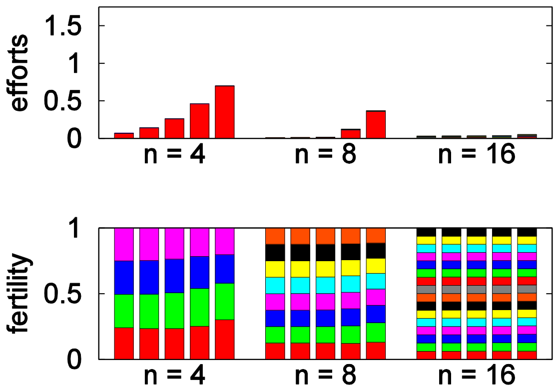


Lowest inequality in the left-most bars; highest inequality in the right-most bars.
Color specifies individual rank: #1 in red, #2 in green, #3 in blue, etc

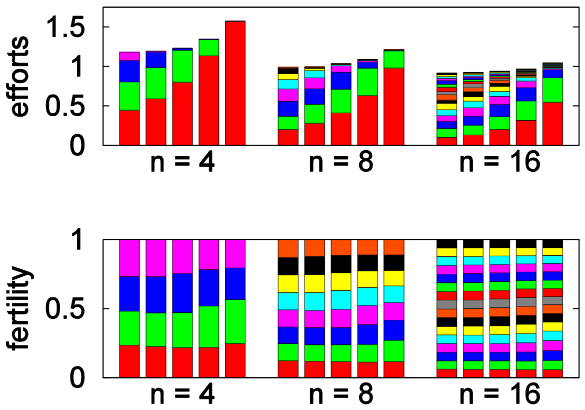
Us vs. nature games: no group extinction

- Individuals defect if rewards are small but cooperate in securing big rewards.
- A threshold effect: individuals contribute only if their valuation is above a certain critical value
- Increasing the reward size causes an increase in the efforts of high valuators but it can also decrease the efforts of low valuators.
- Increasing inequality decreases the efforts of low valuators but this is overcompensated by increased efforts of high valuators.
- The group effort increases with inequality and decreases with group size.

No group extinction



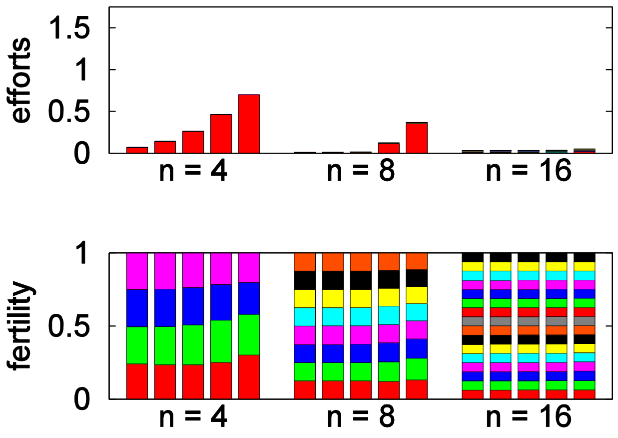
With group extinction



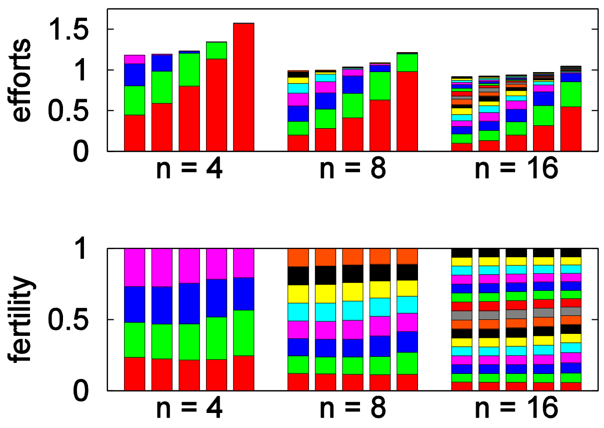
Us vs. nature games: with group extinction

- All group members contribute proportionally to their valuations.
- Individual and group efforts as well as the degree/probabilities of success significantly increase.
- In most cases, individual share of reproduction grows with rank/valuation. But there are some cases, where highest valuators (who are simultaneously the biggest contributors) have lower fertility than other individuals because of the costs paid.
    - “Apparent altruism”; ”altruistic bullies”

No group extinction



With group extinction



Results:

- "Us versus nature" game with nonlinear costs $-c^{\beta}$
  - Benefit-to-cost ratio $r_i = \frac{b_i}{c_i X_0^2}$; $R = \sum r_i$
  - Normalized group effort $Z = \frac{X}{X_0}$
  - Individual efforts $\sim (r_i)^{\frac{1}{\beta-1}}$
  - Normalized group effort Z solves $\beta Z^{\beta-1}(Z+1)^2 = Rn^{\beta-2}H_{\beta-1}$

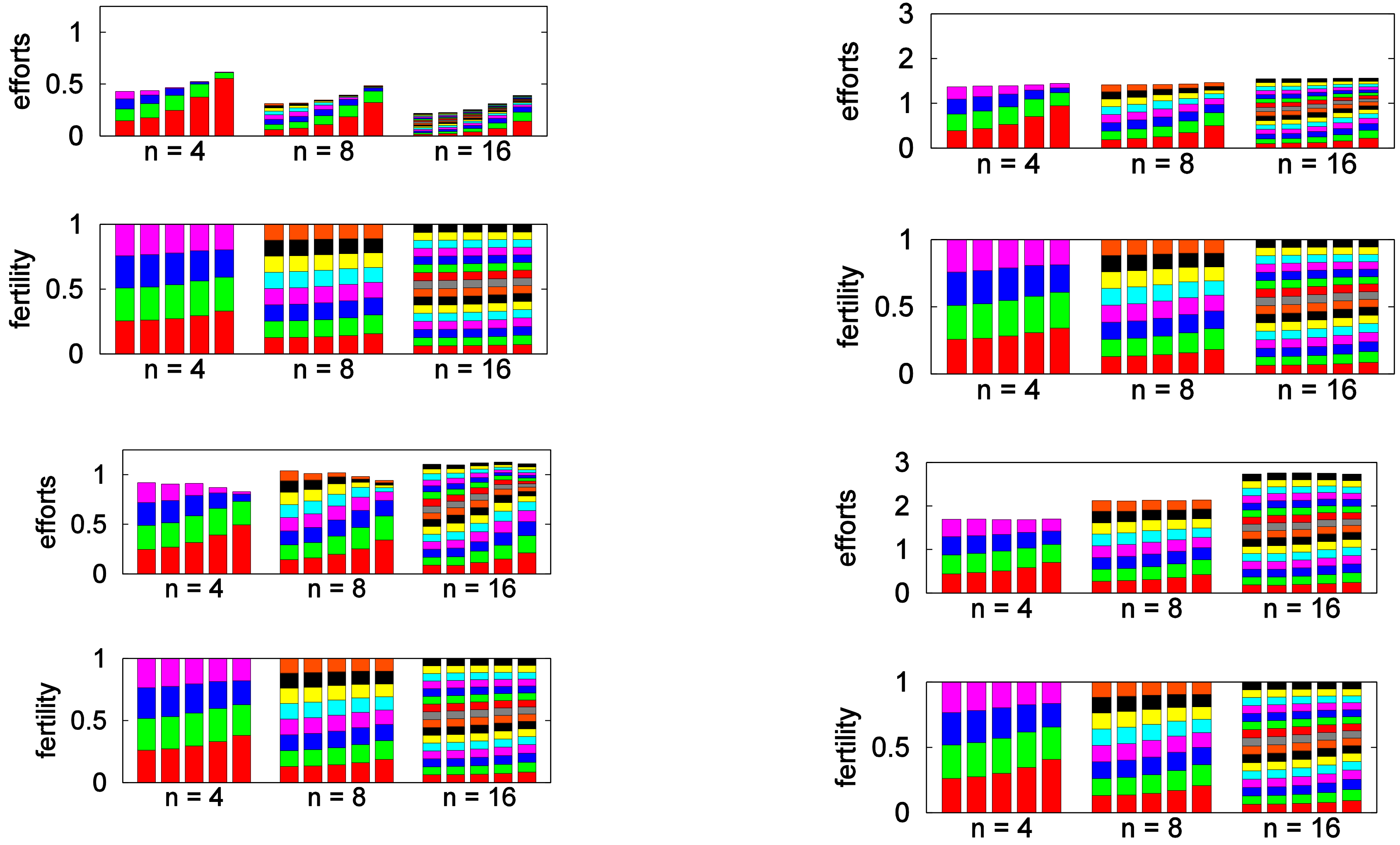
“Us vs. nature”: nonlinear costs $\quad -c_i\, x_i^{\beta}$

No group extinction

With group extinction

$\boldsymbol{\beta = 1.5}$

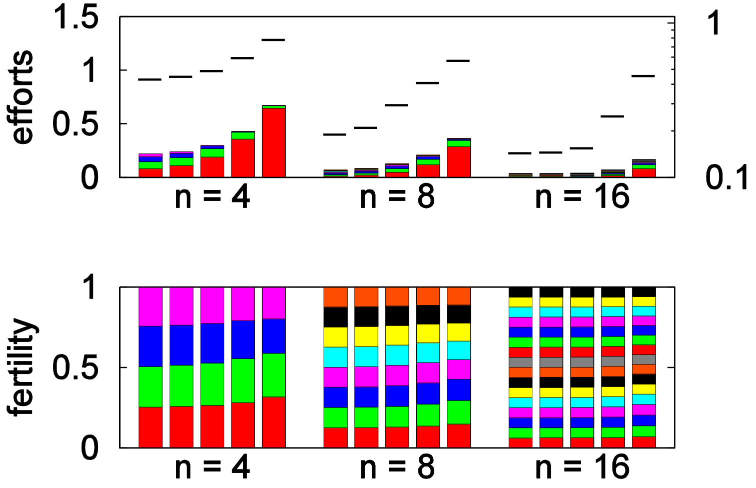
$\boldsymbol{\beta = 2.5}$

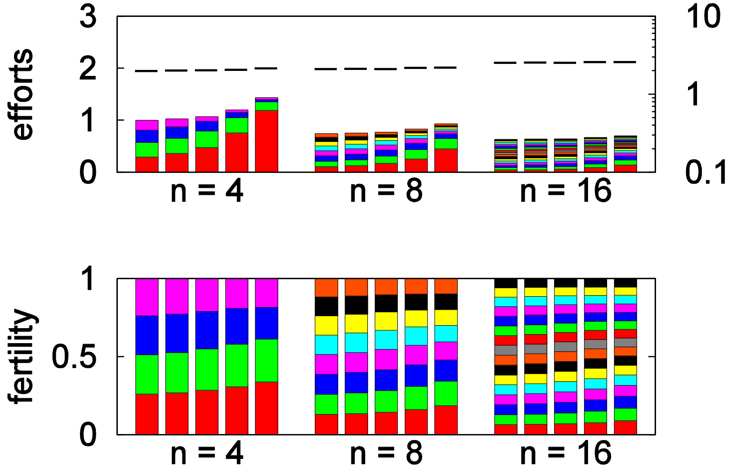


No group extinction

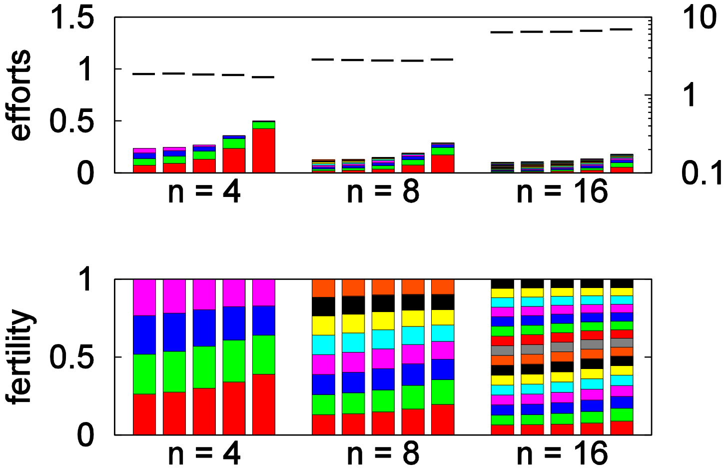
With group extinction

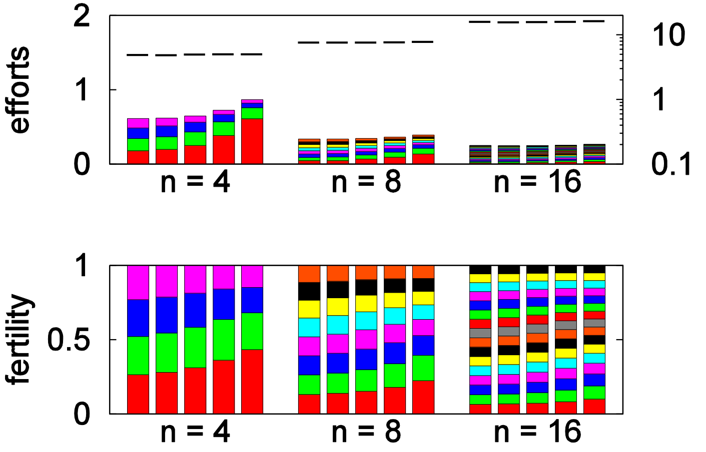
$a = 1.5$





$a = 2.5$

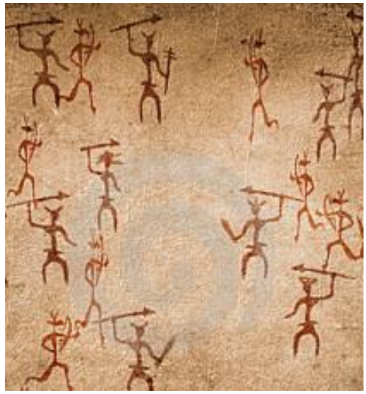




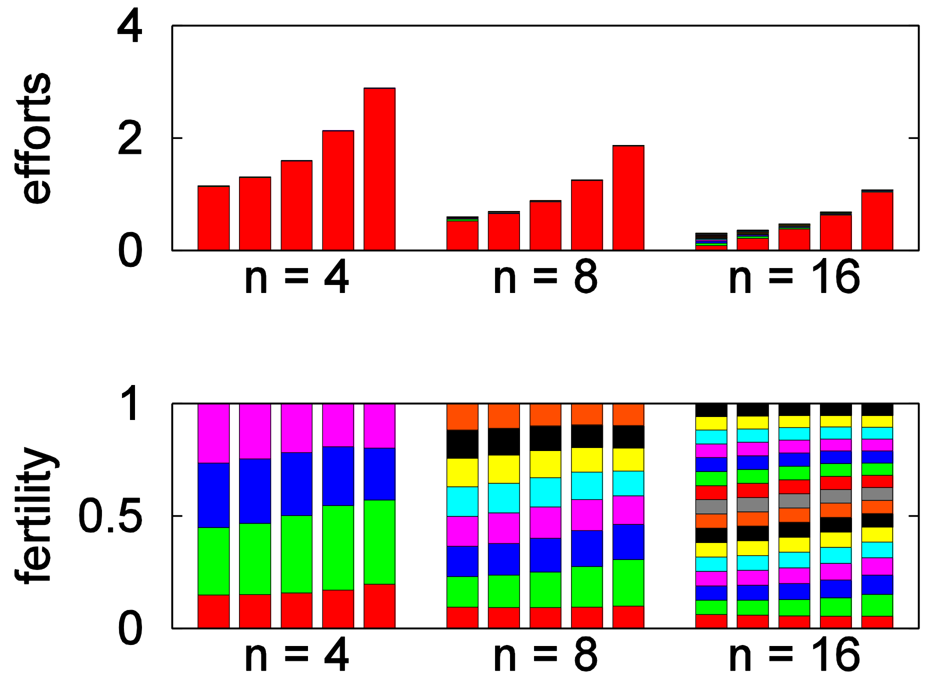
With non-linear impact and cost functions

- With weak nonlinearity in benefit and cost functions (i.e., if α and $\beta < 2$), the group effort typically decreases with group size and increases with within-group heterogeneity.
- With strong nonlinearity in benefit and cost functions (i.e., if α and $\beta > 2$), these patterns are reversed.
- With linear costs, there is high dispersion of efforts within groups. This dispersion is reduced with quadratic costs and, especially, with synergicity.

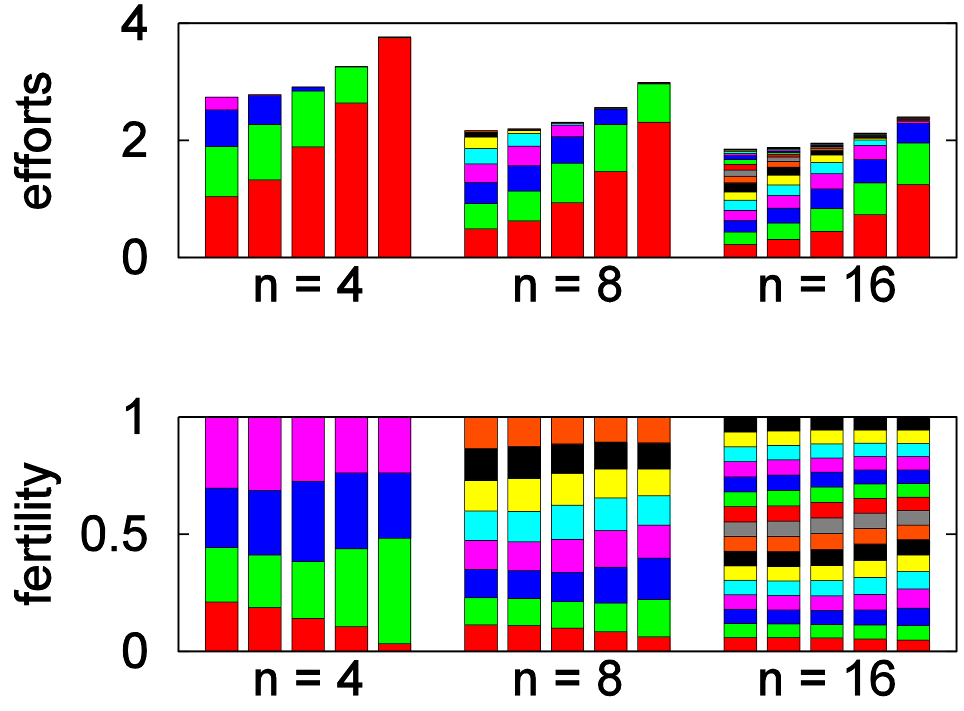
“Us vs. them” games: linear impact and cost functions



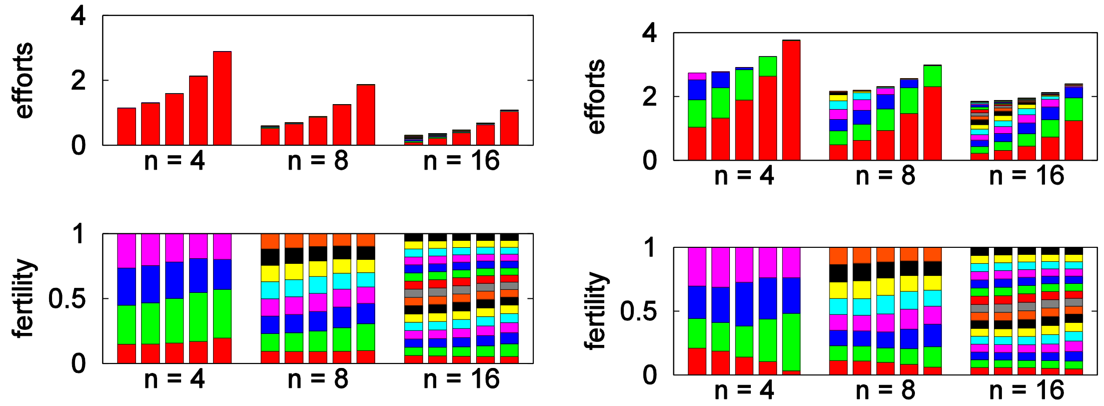
No group extinction



With group extinction

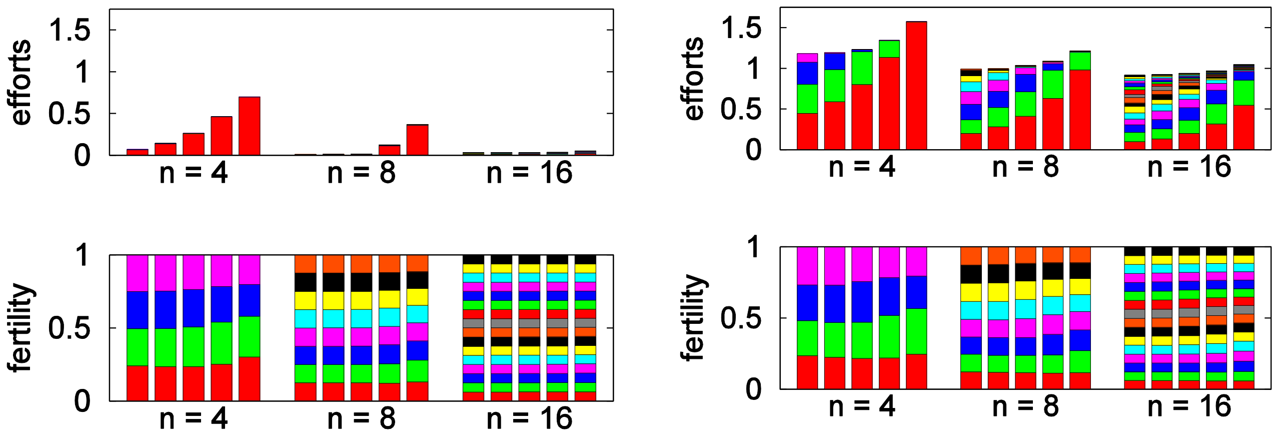


Us vs. them games



- Overall, the behavior of these models parallels that of “us versus nature” models but individual and group efforts are always higher.
- In “us versus nature” games, groups often cooperate only if a corresponding benefit-to-cost ratio exceeds a certain threshold. By contrast, in “us versus them” games, groups always contribute a non-zero effort.
- Direct competition with other groups is much more conducive for the evolution of cooperation than collaboration against nature.

Us versus nature:

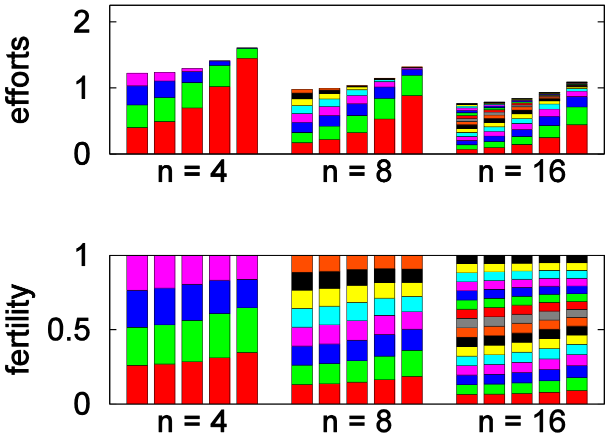


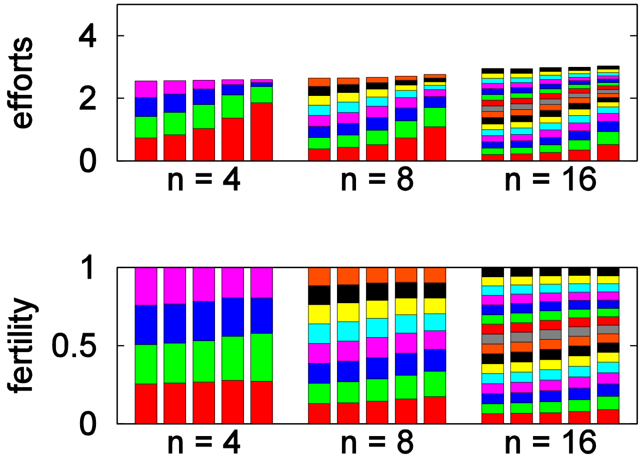
Us vs them: nonlinear costs: $-c_i\ x_i^{\beta}$

No group extinction

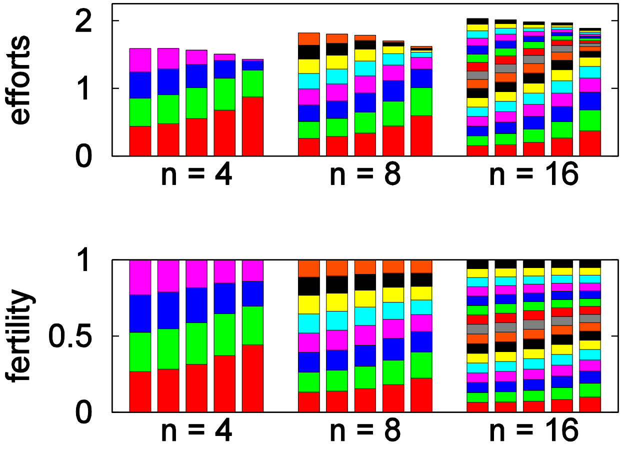
With group extinction

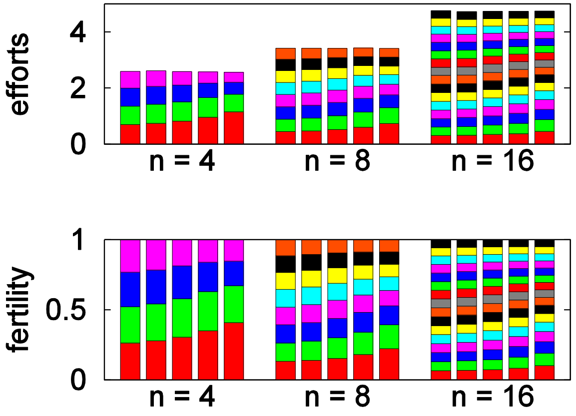
$\boldsymbol{\beta = 1.5}$





$\boldsymbol{\beta = 2.5}$





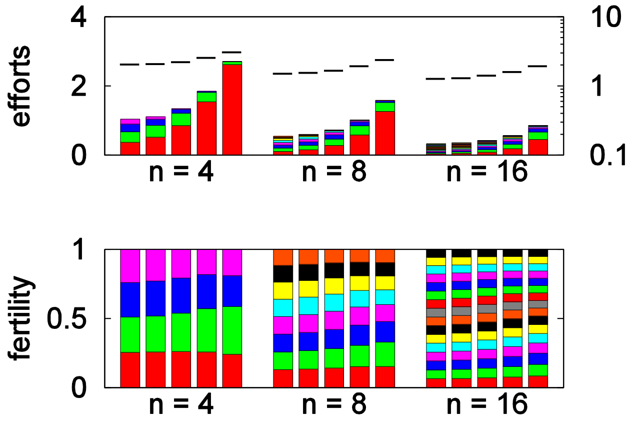
Us vs them; synergicity:

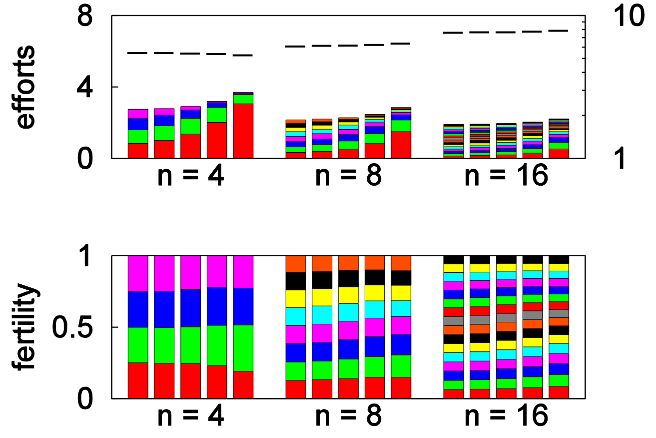
$$X = \left(\sum x_i^{\frac{1}{\alpha}}\right)^{\alpha}$$

No group extinction

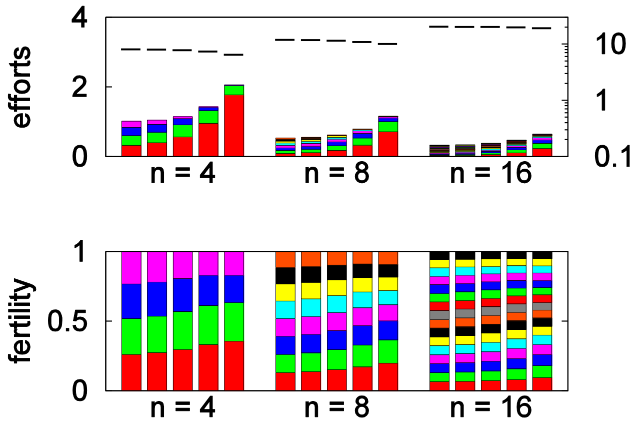
With group extinction

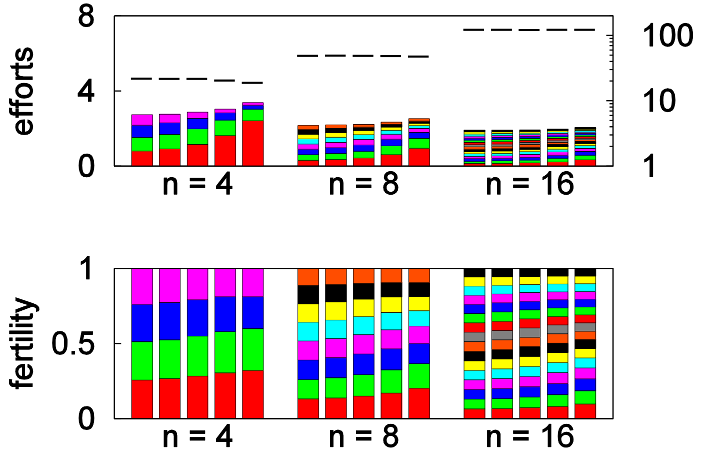
$\boldsymbol{a = 1.5}$





$\boldsymbol{a = 2.5}$





With non-linear impact and cost functions

- With weak nonlinearity in benefit and cost functions (i.e., if α and $\beta < 2$), the group effort typically decreases with group size and increases with within-group heterogeneity.
- With strong nonlinearity in benefit and cost functions (i.e., if α and $\beta > 2$), these patterns are reversed.
- With linear costs, there is high dispersion of efforts within groups. This dispersion is reduced with quadratic costs and, especially, with synergicity.

Generalizations

- Differences in strengths/capabilities
- Differences between groups in sizes and valuations
- Different production functions (e.g., with a ‘decisiveness’ parameter)
- Myopic optimization
- Genetic relatedness

Experimental economics results are inconsistent

- Reviewed in my Phil.Trans.B paper (2015b)

Applications to mammals

- CAPs have been identified in lions, wolves, dogs and many primates
    - Willems & van Schaik: in primates, the only species that do not succumb to the CAP are those that live in relatively small groups with few individuals of the dominant sex, are characterized by philopatry of this dominant sex or are cooperative breeders.
- High valuator effect (“exploitation of the great by the small”)
    - In chimpanzees, high-rank males travel further into the periphery during border patrols and males with higher mating success are more likely to engage in this activity, which is energetically costly.
    - In ring-tail lemurs and blue monkeys, high-rank females participate more in the defense of communal feeding territories than low-rank females.
    - In meerkats, dominant males respond more strongly to intruder scent marks.
    - High-rank chacma baboon males are more likely than low-rank males to join inter-group loud call displays
    - “impact hunters”, “impact patrollers”, “key individuals”
        - “altruistic bullies”

Applications to human origins: conditions for transition to group-wide cooperation

- In us vs. nature, cooperation is successful only if benefit/cost ratio R is big enough; larger collaborative ability α promotes cooperation. A technological change increasing the ability to kill large animals (smaller X_0) or decreasing the danger to hunters (smaller c_i) would make cooperation feasible.
- In us vs. them, a technological innovation allowing for better defense (larger B) would increase efforts; strongly promotes cooperation; more likely to result in group extinction (which helps cooperation).
- Worsening environmental conditions increasing the likelihood of group extinction
- Cultural innovations (e.g. raids with low costs and high benefits)
- Once collaborative skills have been develop in some activities (e.g., hunting and raiding), they can be applied to many other collective actions

Relevance to human psychology

- Humans have a <u>genetic predisposition</u> for collaborative group activities.
  - a consistent observation that human infants are motivated to collaborate in pursuing a common goal
  - cooperative acts result in activation of brain regions involved in reward processing, independently of material gains
- People cooperate when groups face failure because of external threats, e.g. harsh environmental conditions or natural disasters. However cooperation increases dramatically in the presence of direct <u>between-group conflict</u>
  - 'cues of group competition have an automatic or unconscious effect on human behavior that can induce increased within-group cooperation' (Burton-Chellew and West 2012)
- In-group/out-group biases, widespread obsession with team sports, and sex differences in the motivation to form, and skill at maintaining large competitive groups

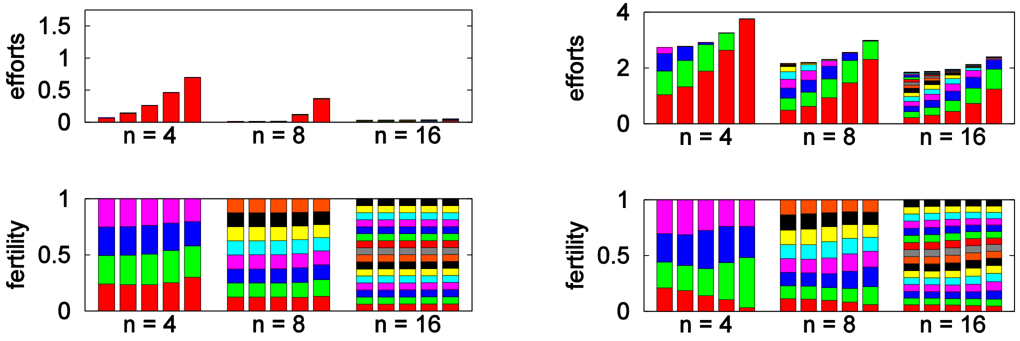
Relevance to human psychology

- Experimental work on “exploitation of the great by the small”
  - more competitive, individualistic players contribute more to collective goods with group competition
  - individuals of high status contribute more towards group goals
  - an arbitrary assignment of an individual to a focal position in the social hierarchy can trigger changes in his/her behavior leading to the endogenous emergence of more centralized forms of punishment.
- In some human groups, the most aggressive warriors have lower reproductive success than other men
  - as documented in the horticulturalist/forager Waorani of Ecuador and Nyangatom of Ethiopia. The Cheyenne war chiefs were expected to be killed in combat, and leaders in the Nyangatom of Ethiopia, the Kapauka of New Guinea, the Jie of Uganda all take greater risks in combat.
- The data show that the highest mortality in the US Army in the Iraq war was among First and Second Lieutenants, who typically lead combat patrols
- Models provide a theoretical justification for a major postulate of the classical equity theory that employees seek to maintain equity between their input-to-output ratio and that of others, and that any variation in these ratios between group members will be viewed as unfair treatment.

Summary of models

- Heterogeneity in
  - Individual costs, endowments, strengths, motivation, valuation
- Games against “nature” or “them”
- With or without group selection
- Individual costs: different types of nonlinearity (β)
- Impact functions: without or with synergicity (α)
  - Evolution of collaborative ability α was explicitly studied in Gavrilets (2015a)

General conclusions



- The largest contributors towards production of collective goods will typically be group members with the highest stake in it or for whom the effort is least costly, or those who have the largest capability or initial endowment.

  - "exploitation of the great by the small" (Olson 1965)

- Under some conditions, such group members end up with smaller net pay-offs than the rest of the group. That is, they effectively behave as altruists (Gavrilets and Fortunato 2014).
  - "Altruistic bully" effect is general
- With weak nonlinearity in benefit and cost functions, the group effort typically decreases with group size and increases with within-group heterogeneity.
  - Inequality can be good for collective action
- With strong nonlinearity in benefit and cost functions, these patterns are reversed.
- 'Under-production' in us vs. nature games; 'over-production' in us vs. them games;
  - us vs. them conflicts are much more conducive for the evolution of cooperation than us vs. nature
- Group extinction greatly amplifies cooperative processes

- Funding