Presentation

The demographic benefits of belligerence and bravery in the island model of warfare: defeated group repopulation or victorious group size expansion?

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Warfare (coalitional aggression) is prevalent in invertebrates and vertebrates

-Termites satisfy the condition of eusociality not because they produce sterile workers but because they produce sterile soldiers.

-Male chimpanzees team up and engage in raids to obtain additional mates and territory.

-In humans, typical tribal societies are supposed to have lost about 5 percent of its population in combat each year.

Large body of litterature on the causes of warfare.

-Irrational explanations (madmen, psychological biases)

-Rational explanations (cost and benefit considerations)

(i) Non-evolutionary (often involves application of standard game theory)

(ii) Evolutionary: are the causes of coaltional aggression genetically determined?

Possible if coalitionary aggression leads to an increase in reproductive enhancing resources to those expressing it.

Warfare is individually costly in time and energy. What are the reproductive enhancing benefits from it?

-Territory, shelters.

- Females.

- Stock of meat, like animal herds, fish.

Several authors have emphasized that warfare has played a fundamental role in human evolution (Hamilton 1975, Durham 1975, Chagnon 1988, Alexander 1990, Gat 2006).

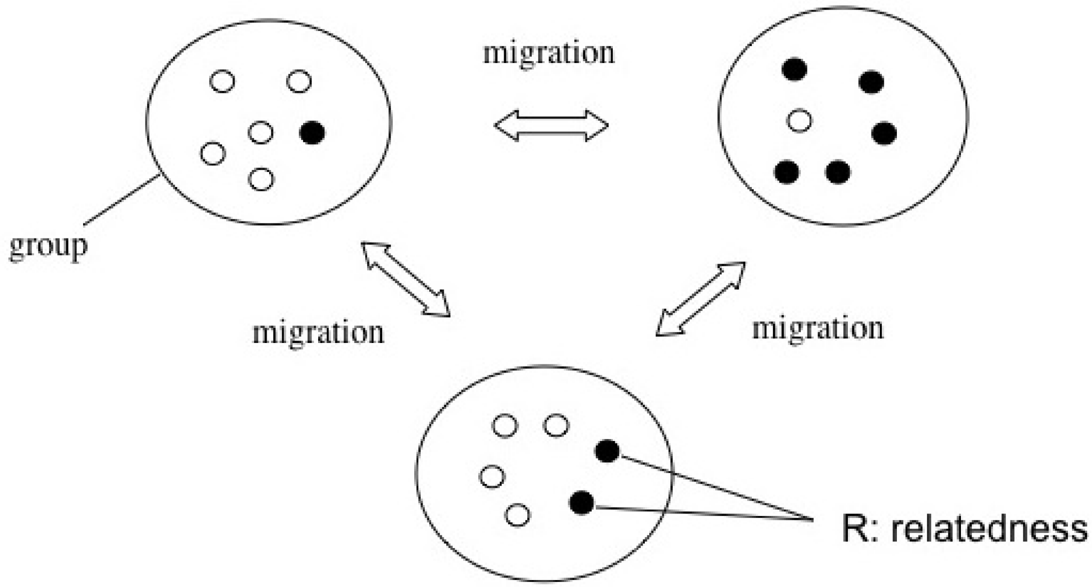
Aim of the talk

-Present an evolultionary game theory model for the co-evolution of belligerence and bravery.

(i) Belligerence : denoted x, increases an actor' s group probability of trying to conquer another group.
(ii) Bravery : denoted y, increase an actors' s group probability of defeating an attacked group.

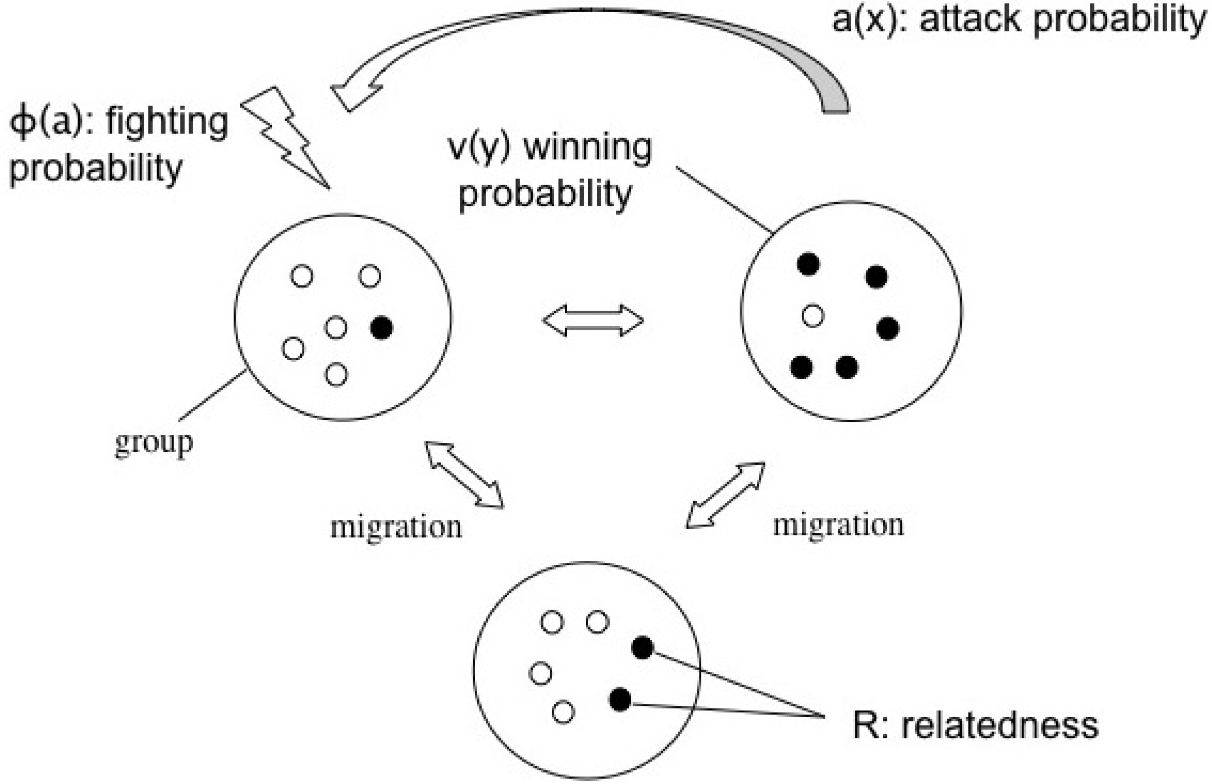
-Assess the strength of selection on the two behaviors as a function of two different types of demographic scenarios: repopulation of defeated groups and local expansion of victorious groups.

Baseline demographic setting underlying the model: structured population with N individuals per group

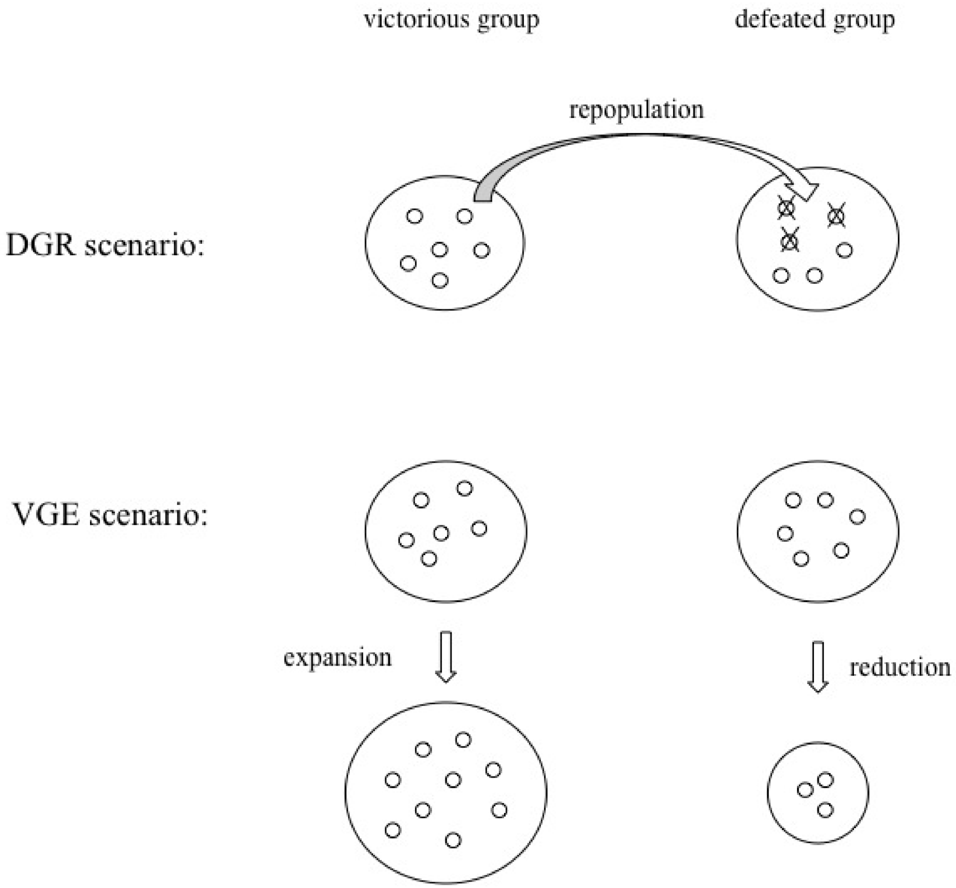


-When groups are of finite size, limited dispersal builds up correlation between gene frequencies within groups: individuals within groups are related.

Island model of warfare: independent attacks and one attack per generation



Two types of demographic scenarios

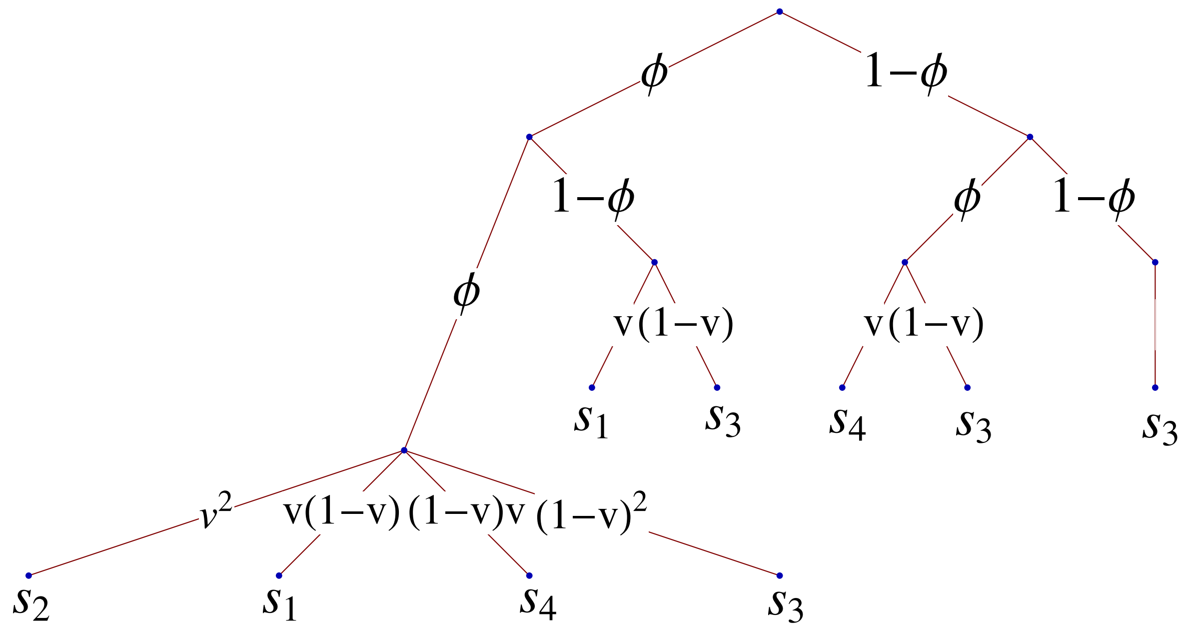


Two types of demographic scenarios with same group level benefits

-Defeated group repopulation (DGR): number of unit of fitness gained at the group level is (1-h)N, where (1-h) is the fraction of defeated group repopulated.

-Victorious group expansion (VGE): number of unit of fitness gained at the group level is (1-h)N, where (1-h)N is the local increase in carrying capacity.

Four possible demographic events for each group under each scenario (DGR and VGE)



"group size" after warfare : $s_1 : [1 + (1 - h)]\,N, \quad s_2 : [h + (1 - h)]\,N, \quad s_3 : N, \quad s_4 : h\,N$

Belligerence, x, determines the fighting probability

$$\phi[x_0, x_1] = a[x_0] \frac{1 - \mathrm{Exp}[-a[x_1]]}{a[x_1]}$$

x_0 : level of belligerence in a focal group.

x_1 : level of belligerence in the population.

a[x] : attack probability, monotonically increasing function of its argument.

Bravery, y, affects the winning probability (contest succes function)

$$v[y_0, y_1, s, s^*] = \frac{\omega\, g[y_0 N_s]}{\omega\, g[y_0 N_s] + (1-\omega)\, g[y_1 N_{s^*}]}$$

y_0 : level of bravery in a focal group.

y_1 : level of bravery in the population.

ω : offensive advantage.

g[k] : power of a contestant, which is an increasing function of its argument.

(i) ratio form $g[k] = k^{\gamma}$, where γ scales the decisiveness of fighting effort disparities.

(ii) difference form $g[k] = \mathrm{Exp}[\gamma\, k]$.

Both belligerence and bravery are individually costly:

Multiplicative cost on fecundity (reproduction)

$$f = (1 - C_x[x_\bullet])\,(1 - C_y[y_\bullet])$$

$x_\bullet$: level of belligerence of a focal individual.

$y_\bullet$: level of belligerence of a focal individual.

Adaptive dynamics of belligerence and bravery

The change in the frequency p of a mutant with phenotype $z_\bullet = z + \delta$ in a population of residents is

$$\Delta p = p\,(1 - p)\,\delta\,S[z] + O[\delta^2]$$

S[z] : growth rate of the mutant in a resident population with trait value z.

The solution of S[z] = 0 provides a candidate ESS.

(Rousset 2004)

DGR scenario: selection gradient on a trait z (either x or y) is given by Hamilton's rule

$$S[z] = \frac{\partial w[z_\bullet, z_0, z_1]}{\partial z_\bullet} + \frac{\partial w[z_\bullet, z_0, z_1]}{\partial z_0} R$$

$w[z_\bullet, z_0, z_1]$: expected number of settled offspring of a focal individual with trait $z_\bullet$.

The derivatives are evaluated at $z_\bullet = z_0 = z_1 = z$.

R : relatedness between groups, which captures the local non-rarity of the mutant.

(Taylor and Frank 1996, Rousset 2004)

DGR scenario: fitness function

$$w = w_p + w_d$$

$$w_p = (1-m)\, f_{\bullet} \left(\underbrace{\frac{1-\phi[x_1, x_1]\, v[y_1, y_0]}{(1-m)\, f_0 + m\, f_1}}_{\text{no local defeat}} + \underbrace{\frac{h\, \phi[x_1, x_1]\, v[y_1, y_0]}{h\,((1-m)\, f_0 + m\, f_1) + (1-h)\, f_1}}_{\text{local loss from defeat}} + \underbrace{\frac{\phi[x_0, x_1]\, v[y_0, y_1]\, (1-h)}{(1-h)\,((1-m)\, f_0 + m\, f_1) + h\, f_1}}_{\text{gain from conquest}} \right)$$

$$w_d = \frac{m\, f_{\bullet}}{f_1}$$

$$f_{\bullet} = (1 - C_x[x_{\bullet}])\,(1 - C_y[y_{\bullet}]),\; f_0 = (1 - C_x[x_0])\,(1 - C_y[y_0]),\; f_1 = (1 - C_x[x_1])\,(1 - C_y[y_1])$$

$$R = \frac{(1-m)^2\,(1 - 2\,\phi\,\omega\,(1-h)\,h)}{N - (1-m)^2\,(N-1)\,(1 - 2\,\phi\,\omega\,(1-h)\,h)}$$

DGR scenario: ES level of belligerence

$$\frac{C_x'}{1 - C_x} = \phi' v \times (1 - h) \times \underbrace{\frac{(1 - m)}{N\left(1 - (1 - m)^2 (1 - 2\phi v (1 - h) h)\right)}}_{\text{Scaled relatedness}}$$

ϕ' v : increase in probability of conquest.

(1 - s) : increase in group reproductive value.

-ES level of belligerence increases as the probability of defeating other group increases.

-ES level of belligerence increases as migration and population size decrease.

DGR scenario: ES level of bravery

$$\frac{C_y'}{1 - C_y} = \phi\, v' \times 2\,(1 - h) \times \underbrace{\frac{(1 - m)}{N\left(1 - (1 - m)^2\,(1 - 2\,\phi\, v\,(1 - h)\,h)\right)}}_{\text{Scaled relatedness}}$$

ϕ v' : increase in probability of conquest.

2(1 - s) : increase in group reproductive value.

$$v' = N\,\omega\,(1 - \omega)\,\frac{g'}{g}$$

Probability of conquest increases with group size!

DGR scenario: ES level of bravery

Ratio form : $g = x^{\gamma} \iff v' = \dfrac{\gamma\,\omega\,(1 - \omega)}{y}$

Difference form : $g = \mathrm{Exp}[\gamma\,x] \iff v' = N\,\gamma\,\omega\,(1 - \omega)$

-If the contest success function is of the difference form, costly bravery may evolve regardless of group size.

(Tullock 1967, Hirshleifer 1989)

VGE scenario: selection gradient

$$S[z] = S_{Pr}[z] + S_f[z]$$

$$S_{Pr}[z] = \sum_{s} \sum_{s'} \left(\nu[s'] \, w_p[s', s] \, \frac{\partial P[s' \mid s]}{\partial z_0} \right) R[s] \, N_s \, P[s]$$

$$S_f[z] = \frac{\partial f_\bullet}{\partial z_\bullet} \sum_{s} \nu[s] \, (1 - R[s]) \, N_s \, P[s]$$

$\nu[s]$: reproductive value of an individual in state s, P[s] : stationary probability of being in state s, R[s] : relatedness in state s. $\nu[s]$ N_s: reproductive value of a group in state s.

(Rousset et Ronce 2004)

VGE scenario: the additional quantities to evaluate

$$\nu[s] = \sum_{s'} \left(w_p[n]\, P[s' \mid s] + \sum_{s^\diamond} w_d[s^\diamond, s]\, P[s' \mid s^\diamond]\, P[s^\diamond] \right) \nu[s']$$

$$P[s'] = \sum_{s'} P[s' \mid s]\, P[s]$$

In order to evaluate the model, we need expressions for the stationary demography.

VGE scenario: complicated transition probabilities

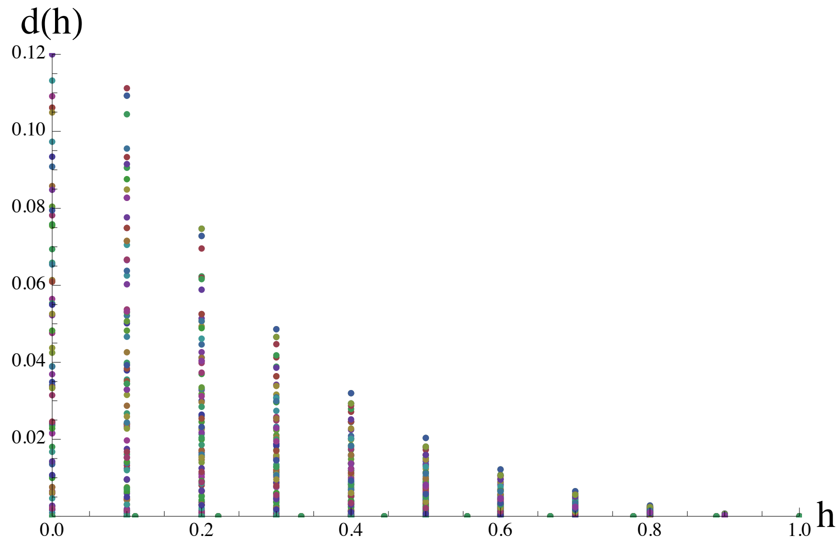
$$P[s_i \mid s] = F[\phi, v[s]]$$

$$v[s] = \sum_{s^*} \frac{\omega\, g[y\, N_s]}{\omega\, g[y\, N_s] + (1 - \omega)\, g[y\, N_{s^*}]}\, P[s^*]$$

VGE scenario: an approximation for the stationary distribution

What about assuming independently distributed demographic events, which occurs when h=1?

$$d[h] = \max_{s} \left| P[s, h] - P[s, 1] \right|$$



Approximation OK for small h.

VGE scenario: ES level of belligerence (assuming h small)

$$\frac{C_x'}{1 - C_x} = \phi' v \times (1 - h)\left(1 - (1 - m)^2\right) \times \underbrace{\frac{(1 - m)}{N\left(1 - (1 - m)^2\right)}}_{\text{Scaled relatedness}}$$

ϕ' v : increase in probability of conquest.

$(1 - h)\left(1 - (1 - m)^2\right)$: increase in group reproductive value.

-Qualitatively the same selection presssure as under the DGR scenario.

-But selection strength lower by than under the DGR scenario.

VGE scenario: ES level of bravery (assuming h small)

$$\frac{C_y'}{1 - C_y} = \phi\, v' \times 2\,(1 - h)\,\left(1 - (1 - m)^2\right) \times \underbrace{\frac{(1 - m)}{N\left(1 - (1 - m)^2\right)}}_{\text{Scaled relatedness}}$$

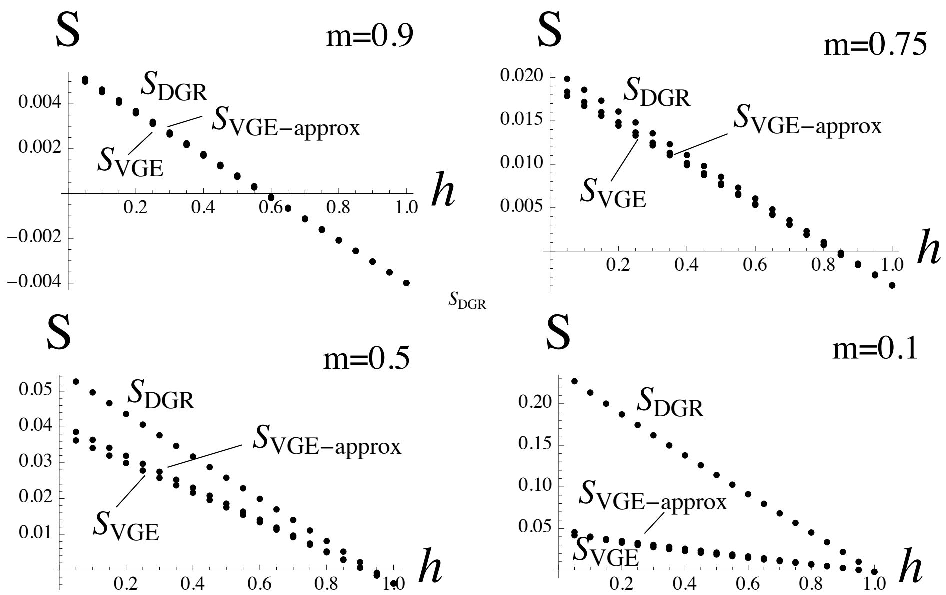
ϕ v' : increase in probability of conquest, where $v' = N\,\omega\,(1 - \omega)\,\frac{g'}{g}$

$2\,(1 - h)\,\left(1 - (1 - m)^2\right)$: increase in group reproductive value.

-Qualitatively the same selection presssure as under the DGR scenario.

-But selection strength lower by than under the DGR scenario.

VGE scenario: stronger benefits



-Selection on the two traits is always stronger under the DGR demographic scenario.
-The approximation of the selection gradient of the VGE scenario is generally good.

Conclusion

-Kinship not only plays its standard effect in determining the individual's sacrifice in the promotion of its group, but it also markedly affects the tendency of individuals within groups to try to take over other ones.

-The selective pressures on belligerence and bravery are strongest when defeated groups can be repopulated by fission of victorious ones, which results in selection being "harder".

-Depending on the form of the contest success function, costly bravery can evolve in groups of any size and thus in large-scale societies. We thus don't need cultural group selection to explain large scale individually costly cooperation.