Boza, Gergely

boza.gergely5@gmail.com
boza@iiasa.ac.at

Eötvös University, Budapest

International Intitute for Applied Systems Analysis (IIASA) EEP, Laxenburg
I am interested in...

- The evolution and stability of mutualism and cooperation
- Continuous reactive investment games
- Conditional, context-dependent cooperation
- Partner choice mechanisms
- Public Good Games with threshold effects
- Division of labor in collective actions
- Stability of microbiomes
- Quorum sensing
- Coexistence and cooperation in early replicator communities
Direct reciprocity

Interacting individuals

1. cost → service → benefit
2. benefit → service → cost
Reciprocity in humans: Economic exchanges
Reciprocity in humans:
food sharing among hunter-gathers
(Aché in Paraguay)
Reciprocity in animals: food sharing in vampire bats (*Desmodus rotundus*)

![Image of vampire bats](image1)

**Figure 1.** Relationships between food donated and predictor variables. Z-score for log food donated was predicted by z-scores of (a) log food received ($R^2 = 0.27$, $p < 0.0002$), (b) allo-grooming received ($R^2 = 0.14$, $p < 0.0002$) and (c) relatedness ($R^2 = 0.04$, $p < 0.0012$). A bubble plot (d) shows multivariate relationships by scaling bubble size to relatedness and bubble darkness to allo-grooming received.

![Graphs showing correlations](image2)

**Figure 3.** Allo-grooming given correlates with allo-grooming received. Allo-grooming giving is plotted against allo-grooming received for dyads that did not share food (a) $n = 214$, $r = 0.62$, $p < 0.0002$ and dyads that did share food (b) $n = 96$, $r = 0.81$, $p < 0.0002$. On non-trial days, dyads that shared food both gave and received more allo-grooming than non-sharing dyads ($F_{1.13} = 32.9$ and $41.0$, $p < 0.0002$ for both).

**Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment**

Gerald G. Carter and Gerald S. Wilkinson

*Proc. R. Soc. B* 2013 **280**, 20122573, published online 2 January 2013
Reciprocity in plants, fungi, bacteria: nutritional mutualisms

Measured sanctions: legume hosts detect quantitative variation in rhizobium cooperation and punish accordingly

E. Toby Kiers, Robert A. Rousseau and R. Ford Denison
Rhizobium etli
Analysis of the metabolic network
• 387 reactions
• 371 metabolites
• 363 genes
Conditional mutualistic investments
The model

\[ I_{1,i,j} = u_i \quad \text{Investment in the 1st round} \]
\[ I_{t,i,j} = u_i + c_i p_{t-1,i,j} \quad \text{Investment in the 1< rounds} \]

\[ C(I_{t,i,j}) = C_0 I_{t,i,j} \]
\[ B(I_{t,j,i}) = B_0[1 - \exp(-B_1 I_{t,j,i})] \]
\[ p_{t,i,j} = B(I_{t,j,i}) - C(I_{t,i,j}) \]

\( t > 1, \text{ iterative game} \)
The evolution and stability of conditional investments

\[ I_t = \alpha + c \cdot \text{payoff}_{t-1} \]

\[ \alpha_1 = \alpha_2 = \text{const.} > 0 \]
The evolution and stability of conditional and unconditional investments

\[ c \text{ zero isocline} \]
\[ u \text{ zero isocline} \]
Unconditional investment, \( u \)

Conditional investment, \( c \)

(closely) monomorphic population
Investment cycle phases

\[ g_{i,x}(x_i) = \partial \left( \frac{1}{J} \sum_{j=1}^{J} P_{i,j} \right) \bigg/ \partial x_i' \bigg|_{x_i'=x_i} \]
Investment cycle and phase polymorphism

\[ g_{i,x}(x_i) = \partial \left( \frac{1}{J} \sum_{j=1}^{J} P_{i,j} \right) / \partial x_i |_{x_i=x_i} \]
Investment cycle and phase polymorphism

Phase of the investment cycle ($\varphi$)

Frequency of phase category

Unconditional investment, $u$

Conditional investment, $c$
Strategy diversity and phase polymorphism stabilizes cooperative investments
Strategy diversity and phase polymorphism stabilizes cooperative investments
Introducing spatial population structure in interspecific reciprocal investment game
Spatial bubbles and the dynamic spatial mosaic structure
Spatial bubbles and invasion dynamics

- Conditional investment, $\log c$
- Unconditional investment, $\log u$
- m $\rightarrow$ R
- coexistence
- R $\rightarrow$ m
Summary

• Cooperative investments are unstable for medium levels of reciprocity
• Above a threshold, evolution drives strategy pairs through investment cycles temporarily
• Mutation-generated polymorphism of strategies leads to phase diffusion along the investment cycle
• Strategy diversity (polymorphism) stabilizes investment levels at the population level
• Spatial mosaic structure further promotes mutualism stability, through a mechanism that is fundamentally different from the role of space in intraspecies cooperation
Non-linear benefit functions and threshold effects in nature

**lions** (*Panthera leo*)

from Packer *et al.* (1990) and Stander (1992)
Non-linear benefit functions and threshold effects in nature

Harris’ Hawk (*Parabuteo unicinctus*)

Brown-Necked Raven (*Corvus ruficollis*)

from Bednarz (1988)

Yosef & Yosef (2009)
Non-linear benefit functions
and threshold effects in nature

killer whales (*Orcinus orca*)
humpback whales (*Megaptera novaengliae*)

from Leighton *et al.* (2004)
Non-linear benefit functions and threshold effects in nature

from Hibbing et al. (2010)
Non-linear benefit functions
and threshold effects in nature
The Threshold Public Good Game

Score

T
R

Number of cooperators

Threshold value (T)

D
C

0
Threshold Public Good Game

Well–mixed population

Group size ($N$) 3

Threshold value ($T$) 2

Cost of cooperation ($C(x)$) $x$ -axis

Benefit of cooperation ($b$) 1

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<td>D</td>
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Individual willingness to cooperate ($x$) is a continuous, evolving trait.

$x = 1 \quad \rightarrow \quad always\ cooperate$

$x = 0 \quad \rightarrow \quad always\ defect$

following Bach et al. (2006)
Polymorphic equilibria, bifurcation, hysteresis point

\[ C(x) \] – cost of cooperation

\[ T \text{ (threshold value)} = 2 \]

\[ N \text{ (group size)} = 3 \]
Group size

4

5

6

7

9
Hysteresis point and the sigmoid return function

\[ P(x) = \frac{1}{1 + e^{-(n-T) * (-s)}} \]

- **s** – steepness

Number of cooperators in the group

\[ N=5 \]

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Probability of public good produced

Number of cooperators in the group

\[ C(x) \]
Group cooperation and inter-group conflict
Population structure and multilevel selection

\( N = 5 \quad T = 3 \)

- \( x \) – willingness to cooperate during cooperative hunting
- \( a \) – willingness to cooperate during group defence

\[ (DD) \quad (CC) \quad (CD) \quad (CD;DC) \]
Summary

• Non-linear payoff functions are more suited for many phenomena in nature
• Stable polymorphism, coexistence of cooperators and defectors
• Spatial population structure promotes cooperation
• Division of labor in multi-public good games
• Context dependent cooperation (cooperators vs. laggards) assuming intra-group cooperation and inter-group conflict
• Not all non-cooperators are in fact „full” cheaters
Spread of beneficial and parasitic microorganisms in host mediated microbiomes
Non-linear dosage-effect function of antibiotics

from Hibbing et al. (2010)
Leaf-cutter ant microbiome
Modelling antibiotics producing bacteria

Dynamics of the antibiotics in the environment

\[ A_{\text{Env},i}^{t+\Delta t} = A_{\text{Env},i}^t + \left[ \frac{D}{\Delta x^2} \left( \sum_{j \in \text{nn}} A_{\text{Env},j}^t - 4A_{\text{Env},i}^t \right) + \rho_{\text{pr}/\tau} - \mu^i A_{\text{Env},i}^t + \delta^i A_{\text{Int},i}^t - \phi^i A_{\text{Env},i}^t \right] \Delta t \]

Intracellular dynamics of the antibiotics

\[ A_{\text{Int},i}^{t+\Delta t} = A_{\text{Int},i}^t + \left[ \mu^i A_{\text{Env},i}^t - \delta^i A_{\text{Int},i}^t - \lambda^i A_{\text{Int},i}^t \right] \Delta t \]

Reproduction rate of the producer (A+R+)

\[ r_{i}^{A+R+} = r_{0}^{A+R+} + r_{\text{pr}}(t) - c_{AR} \]

Reproduction rate of parasite (A-R-)

\[ r_{i}^{A-B-} = r_{0}^{A-B-} + r_{\text{pr}}(t) - \gamma(\alpha, T, A_{\text{Int},i}) \]
Antibiotics producing vs parasitic bacteria

- **A+R+**
- **A-R-**
Antibiotics producing vs parasitic bacteria

- A+R+
- A-R-
Antibiotics producing vs parasitic bacteria
Thank you for your attention!