Evolution of Cooperation with Stochastic Non-Participation

Alex Ginsberg

Dartmouth College Research Experience for Undergraduates in Mathematical Modeling in Science and Engineering

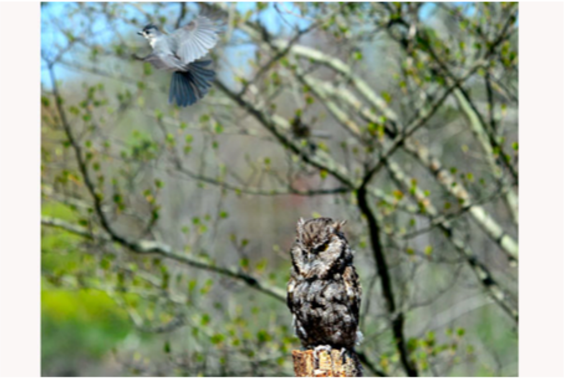
August 17, 2017

Table of Contents

1. Introduction
   - Cooperation
   - Public Goods Games
2. The Model
   - Tweak to the Standard Public Goods Game
   - Example
   - Pairwise Comparison: the details
3. Results
   - Expected Payoffs
   - Probabilities of Updating
   - Fixation Probabilities
   - Threshold Return on Investment by Cooperators
   - Properties of R
4. Further Study
5. References

Cooperation

- Cooperation is everywhere
- Bacteria cooperate to form biofilms
- Birds cooperate by sounding the alarm when a predator is nearby
- People cooperate all the time, such as when people bring food to a potluck



At an experiment conducted in Ithaca, New York, a Tufted Titmouse was the first to spot and sound the alarm about the appearance of an Eastern Screech-Owl roboraptor. *Photo by Tim Gallagher.*

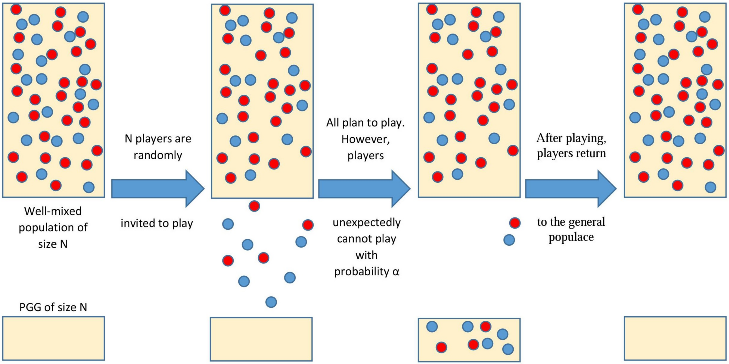
Photo from article by Axelson, G. (See References)

Public Goods Games

- Public Goods Games (PGGs) are everywhere
- Biofilms created by bacteria (in some cases) are a public good for bacteria
- Bird alarms are a public good for wildlife
- Food at a potluck is a public good for the potluck-goers

Tweak to the Standard PGG

- Have well-mixed population of n individuals
- N players are invited to participate in a PGG
- All will accept the offer, and decide beforehand whether they will cooperate or defect
- Cooperators invest 1 unit. That unit is multiplied by a factor r and placed in a common pool
- Defectors free-ride
- The common pool is then distributed among all players
- Unlike in the standard model, where everyone who accepts the offer plays, some people here do not play due to unforeseen circumstances
- Each individual does not play due to unforeseen circumstances with probability α



Cooperators (blue) and defectors (red) exist in a heterogeneous population represented by the large tan rectangular area. Frequently a fixed number of players are offered to opportunity to participate in a PGG, represented by the small tan rectangular area, and they all accept. While most players are able to make it to the game, some are not. Players then return to the general populace, where no game is occurring

Example

- Suppose you are one of N people invited to a party
- Like everyone else, you accept the invitation
- Each person invited is asked to bring some menu item
- Each person decides beforehand whether they will cooperate and bring food or defect and bring nothing
- All people then share the food brought to the party more or less equally
- However, some people are no-shows. Perhaps they got sick or realized that they had procrastinated their homework too much

- In a conversation with a friend you discuss your feelings about bringing (or not bringing) food
- At the end of the conversation, you decide that if your friend was happier, you will probably adopt their strategy
- However if you were happier than your friend, you will probably keep your strategy

- The process described in the preceding example is the pairwise comparison process we discussed in class
- Players occasionally update their strategies via *Pairwise Comparison*

Pairwise Comparison: the details

- One player randomly selected for updating
- Other player randomly selected for Comparison
- Player selected for updating switches strategies with probability p proportional to payoff difference
- $p = 1/2 + \frac{\gamma}{2} \frac{\pi_{com} - \pi_{up}}{|\pi_{com} - \pi_{up}|}$
  - Recall from class that this is the probability in the limit of weak selection given payoffs given fitness $1 - \gamma + \gamma * payoff$
- π_{com} is expected payoff of individuals playing the strategy of the individual selected for comparison,
- π_{up} represents the expected payoff of individuals playing the strategy of the individual selected for updating
- $0 < \gamma << 1$

Expected Payoffs

- Let π_d be the expected payoff for defectors
  - $\pi_d = \alpha\sigma + (1-\alpha)[rx_c[1-(1-\alpha^N)/(1-\alpha)] + \alpha^{N-1}\sigma]$
- x_c is the proportion of cooperators in the population
- Let π_c be the expected payoff for cooperators
  - $\pi_c = \pi_d + r/n[\alpha(1-\alpha^{N-1})] + (1-\alpha)[-1+(1-r)\alpha^{N-1} + (r/N)(1-\alpha^N)/(1-\alpha)]$
- $\pi_c - \pi_d = r/n[\alpha(1-\alpha^{N-1})] + (1-\alpha)[-1+(1-r)\alpha^{N-1} + (r/N)(1-\alpha^N)/(1-\alpha)]$

Probabilities of Updating

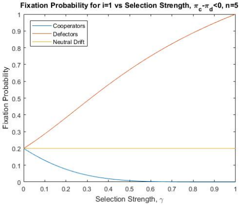
- Let p_{cd} be he probability that the number of cooperators decreases by one in an iteration
- Then:
  - $p_{cd} = 1/2 - \frac{\gamma}{2} sign(r/n[\alpha(1-\alpha^{N-1})] + (1-\alpha)[-1+(1-r)\alpha^{N-1} + (r/N)(1-\alpha^{N})/(1-\alpha)])$
- Let p_{dc} be the probability that the number of cooperators increases by one in an iteration
- Then:
  - $p_{dc} = 1/2 + \frac{\gamma}{2} sign((1-\alpha)[-1 + (1-r)\alpha^{N-1} + \frac{r}{N}\frac{1-\alpha^{N}}{1-\alpha}])$

Fixation Probabilities

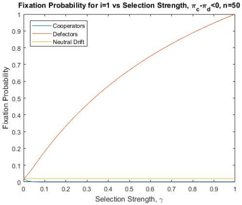
- $x_i = (1 + \Sigma_{j=1}^{i-1} \Pi_{k=1}^{j} p_{cd}/p_{dc})/(1 + \Sigma_{j=1}^{n-1} \Pi_{k=1}^{j} p_{cd}/p_{dc})$
- Let $G = p_{cd}/p_{dc} = (1 - \gamma * sign(\pi_c - \pi_d))/(1 + \gamma * sign(\pi_c - \pi_d))$
- Note that G is constant

- Expanding G as a geometric series, we obtain:
    - $x_i = (1 - G^i)/(1 - G^n)$
- To obtain the fixation probability for defectors, simply replace G with 1/G. Then:
    - $y_i = [G^i - G^n]/[1 - G^n]$
- Note that $x_i + y_{n-i} = 1$
- We always have fixation of either the mutant or the invader.

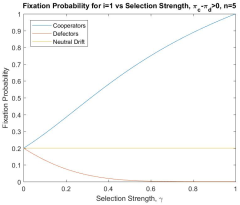
- It can be demonstrated analytically that there are three possibilities:
  - Cooperation is favored by natural selection over neutral drift, and neutral drift is favored over defection $(\pi_c - \pi_d > 0)$
  - Neither cooperation nor neutral nor defection are favored one over the other by natural selection, $(\pi_c = \pi_d)$, or
  - Defection is favored by natural selection over neutral drift, and neutral drift is favored over cooperation $(\pi_c - \pi_d < 0)$.


Fixation Probability for i=1 vs Selection Strength, π_c-π_d<0, n=5
Cooperators
Defectors
Neutral Drift
Fixation Probability
Selection Strength, γ

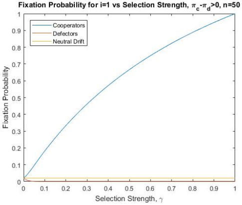
(a)


Fixation Probability for i=1 vs Selection Strength, π_c-π_d<0, n=50
Cooperators
Defectors
Neutral Drift
Fixation Probability
Selection Strength, γ

(b)


Fixation Probability for i=1 vs Selection Strength, π_c-π_d>0, n=5
Cooperators
Defectors
Neutral Drift
Fixation Probability
Selection Strength, γ

(c)


Fixation Probability for i=1 vs Selection Strength, π_c-π_d>0, n=50
Cooperators
Defectors
Neutral Drift
Fixation Probability
Selection Strength, γ

(d)

Threshold Return on Investment by Cooperators

- We can now choose a threshold value of r, R, for given N, n, and α such that:
  - $r > R$ implies that $\pi_c - \pi_d > 0$
  - $r < R$ implies that $\pi_c - \pi_d < 0$
  - $r = R$ implies that $\pi_c - \pi_d = 0$
- $\pi_c - \pi_d > 0 \Leftrightarrow r > \dfrac{1-\alpha^{N-1}}{[\alpha(1-\alpha^{N-1})]/[n(1-\alpha)] + [1-\alpha^N]/[N(1-\alpha)] - \alpha^{N-1}} = R(\alpha)$

Properties of R

- $R < N$ on $[0, 1)$
- R is defined on $[0, 1)$
- R is continuous on $[0, 1)$
- R is strictly decreasing on $[0, 1)$
- So, increasing α lowers R, facilitating cooperation

Further Study

- Further analysis of R
- Adaptive Dynamics
  - A few changes to the model
    - N=2
    - Players play only one strategy initially, which involves cooperating with a fixed probability
    - A single mutant with a very similar strategy invades.
    - The mutant will either fixate or dies out.
    - Repeat
  - For what very similar strategies does the mutant have the highest fixation probabilities?

References

- Hauert, C., De Monte, S., Hofbauer, J. and Sigmund, K., 2002. Replicator dynamics for optional public good games. Journal of Theoretical Biology, 218(2), pp.187-194.
- Hauert, C., De Monte, S., Hofbauer, J. and Sigmund, K., 2002. Volunteering as red queen mechanism for cooperation in public goods games. Science, 296(5570), pp.1129-1132.
- Sigmund, K., De Silva, H., Hauert, C. and Traulsen, A., 2010. Social learning promotes institutions for governing the commons.
- Nadell, C.D., Xavier, J.B., Levin, S.A. and Foster, K.R., 2008. The evolution of quorum sensing in bacterial biofilms. PLoS biology, 6(1), p.e14.
- Imhof, L.A. and Nowak, M.A., 2010. Stochastic evolutionary dynamics of direct reciprocity. Proceedings of the Royal Society of London B: Biological Sciences, 277(1680), pp.463-468.
- Hauert, C., Traulsen, A., née Brandt, H.D.S., Nowak, M.A. and Sigmund, K., 2008. Public goods with punishment and abstaining in finite and infinite populations. Biological theory, 3(2), pp.114-122.
- Pacheco, J.M., Vasconcelos, V.V., Santos, F.C. and Skyrms, B., 2015. Co-evolutionary dynamics of collective action with signaling for a quorum. PLoS computational biology, 11(2), p.e1004101.
- Nowak, M., 2006. Evolutionary Dynamics: Exploring the Equations of Life. Harvard University Press, ch. 6.
- Axelson, G., 2016. Look out! The Backyard Bird Alarm Call Network. Living Bird Magazine, Winter 2016 Issue. [Accessed from https://www.allaboutbirds.org/look-out-the-backyard-bird-alarm-call-network/].