



# Fast cheater migration stabilizes coexistence in a public goods dilemma on networks

Glenn Young\*, Andrew Belmonte

Department of Mathematics, Pennsylvania State University, University Park, PA 16802, United States

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## ABSTRACT

Through the lens of game theory, cooperation is frequently considered an unsustainable strategy: if an entire population is cooperating, each individual can increase its overall fitness by choosing not to cooperate, thereby still receiving all the benefit of its cooperating neighbors while no longer expending its own energy. Observable cooperation in naturally-occurring public goods games is consequently of great interest, as such systems offer insight into both the emergence and sustainability of cooperation. Here we consider a population that obeys a public goods game on a network of discrete regions (that we call colonies), between any two of which individuals are free to migrate. We construct a system of piecewise-smooth ordinary differential equations that couple the within-colony population dynamics and the between-colony migratory dynamics. Through a combination of analytical and numerical methods, we show that if the workers within the population migrate sufficiently fast relative to the cheaters, the network loses stability first through a Hopf bifurcation, then a torus bifurcation, after which one or more colonies collapse. Our results indicate that fast moving cheaters can act to stabilize worker–cheater coexistence within network that would otherwise collapse. We end with a comparison of our results with the dynamics observed in colonies of the ant species *Pristomyrmex punctatus*, and argue that they qualitatively agree.

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## 1. Introduction

Public goods dilemmas occur when an individual must choose whether or not to contribute to a commonly available (public) good (Archetti and Scheuring, 2012; Fehr and Gächter, 2000; Hauert et al., 2008; Oakland, 1987; Perc et al., 2013; Wakano et al., 2009). Contributing benefits the population by increasing the total amount of the public good, but it comes at a cost to the individual (through energy expenditure, for example), whereas choosing not to contribute comes at no cost to the individual, who still shares in benefits from the public good. Thus individuals must choose between what is best for themselves and what is best for the population, and in the basic public goods game, benefitting without contributing is strictly speaking always the better choice (Archetti and Scheuring, 2012; Perc et al., 2013). Consequently, the dilemma inherent in public goods games have been used as a framework for studying the origin of cooperation and other group interactions (Archetti and Scheuring, 2012; Levin, 2014). Such dilemmas are most naturally found in biological systems involving populations living closely enough together so that individual efforts are inevitably shared, for instance in bacterial species (Damore and

Gore, 2012) such as *Escherichia coli* (Vulić and Kolter, 2001) and *Myxococcus xanthus* (Velicer et al., 2000), in social insects such as ants (Dobata et al., 2011) and bees (Martin et al., 2002), and even in tumor cells, in which a subpopulation of cells produce an insulin-like tumor growth factor (Archetti et al., 2015; Gerlee and Altrock, 2017). While some such systems manage to persist in the presence of parasitic genetic cheaters (e.g., the queenless ant species *Pristomyrmex punctatus*, Dobata et al., 2011), others collapse (e.g., the Cape honey bee Martin et al., 2002), leading to the natural question of what mechanisms foster these two outcomes. Many such mechanisms for sustaining cooperation have been studied, most notably kin selection (Hamilton, 1964; Lehmann and Rousset, 2014), rewarding cooperation (Szolnoki and Perc, 2010) and punishing defection (Fehr and Gächter, 2000; Riehl and Fredrickson, 2016), or through interspecies competition: competition with a common opponent can stabilize cooperation within a public goods game within microbial species (Celiiker and Gore, 2012). Kin selection is often quantified by Hamilton's rule: it is beneficial for an individual to behave altruistically toward another individual if the product of the increase in offspring of the recipient and the genetic relatedness of the two is greater than the reproductive cost of the altruistic act (Hamilton, 1964). Hamilton's rule helps explain the evolution of altruism, especially in social insects such as ants, bees, and wasps (Lehmann and Rousset, 2014), though it is usually

\* Corresponding author.

E-mail address: [gsy4@psu.edu](mailto:gsy4@psu.edu) (G. Young).

not used to address the stable existence of parasitic cheaters, as in the case of *Pristomrymex punctatus*. Aside from kin selection, no other cooperation-stabilizing mechanism has been observed in either of the previously mentioned ant or bee systems (Dobata and Tsuji, 2013; Martin et al., 2002), indicating that there are still unexplored mechanisms by which cooperation can be sustained.

Our focus is on species that reproduce via parthenogenesis and occupy two or more discrete regions, such as colonies, between which individuals are free to migrate. Parthenogenesis is a form of asexual reproduction in which an embryo develops into an organism without fertilization, and consequently offspring are clones of their mother (Mittwoch, 1978). This simplifies the task of mathematically modeling reproductive competition due to phenotypic variations, as genetic variability is minimized between generations. Moreover, parthenogenetic reproduction is common in nature, and has been observed in species ranging from aphids (Simon et al., 2002), ants (Dobata et al., 2011; Dobata and Tsuji, 2013; Tsuji and Dobata, 2011), and bees (Martin et al., 2002) to zebra sharks (Dudgeon et al., 2017) and Komodo dragons (Watts et al., 2006).

Migration often plays a large role in many species' survival. Driven by internal or external stimuli, species as simple as bacteria (Turnbull et al., 2001) to complex organisms such as fish (Partridge, 1982), birds (Thompson et al., 1974), and countless others depend on their collective ability to migrate to evade environmental or ecological stress. Mathematical models for migration have expanded our understanding of the formation of spatial patterns in bacteria (Tyson et al., 1999), flocking behavior of birds (Heppner and Grenander, 1990), and colony-site selection in honeybees (Reina et al., 2017). Here, we develop a mathematical model connecting the well-studied fields of public goods games and migratory dynamics to study the stabilization of cooperation by migration in populations with genetic cheaters.

For the remainder of this paper, we will call the individuals that cooperate “workers”, those that do not “cheaters”, and the discrete regions they occupy “colonies”. To model the role that cheaters play in such populations, we propose a mathematical model coupling within-colony population dynamics and between-colony migratory dynamics. While our model shows that cheaters drive down the fitness of an individual colony, it also makes the unexpected prediction that fast cheaters can actually stabilize a network of colonies by saving individual colonies from collapse. The remainder of this paper is organized as follows: in the following section, we develop a system of ordinary differential equations modeling the population dynamics of workers and cheaters in a network of  $N$  colonies, connected according to a given connectivity matrix  $B$ . We then analyze the behavior of a single colony, to determine conditions under which workers and cheaters can coexist. In Section 3, we begin our investigation of the effects of migration by considering a two-colony network, between which the worker and cheater populations are free to travel, and determine conditions under which the two colonies can be maintained, and conditions under which it collapses into a single colony. Section 4 builds on the results and intuition of the two-colony system to determine similar conditions under which an  $N$ -colony, all-to-all connected network collapses. Finally, we consider  $N$ -colony networks connected according to more complicated graph structures, and discuss the implications of our results.

## 2. Model construction

In this section, we develop a model of within- and between-colony dynamics of a parthenogenetically reproducing organism. We generally consider a collection of  $N$  colonies, which we will hereafter refer to as a colony network, or simply a *network*, in which individual colonies are connected according to a given connectivity structure.

Within colony  $i = 1 \dots N$ , the population is comprised of two sub-populations: *workers*, whose density is denoted by  $u_i$ , who contribute to the public good at rate  $c$ , and *cheaters*, whose density is denoted by  $v_i$ , who do not contribute. We assume the populations  $u_i$  and  $v_i$  grow at rates proportional to the available public good, have respective natural mortality rates  $\mu_u$  and  $\mu_v$ , and suffer fecundity loss due to crowding rate  $\gamma_i(u_i + v_i)$ . For full generality, we will initially assume that the public good is a dynamic variable, denoted  $\phi_i$  (Allen et al., 2013). The public good is produced only by workers, though it is consumed by both populations at rate  $\kappa$ , and naturally spoils at rate  $\delta$ . With these assumptions, the population model within colony  $i$  is

$$\begin{aligned}\dot{u}_i &= u_i [\tilde{r}_u \phi_i - c - \gamma_i(u_i + v_i) - \mu_u] \\ \dot{v}_i &= v_i [\tilde{r}_v \phi_i - \gamma_i(u_i + v_i) - \mu_v] \\ \dot{\phi}_i &= cu_i - [\kappa(u_i + v_i) + \delta] \phi_i.\end{aligned}\quad (1)$$

The crowding term allows for an interior coexistence equilibrium within each colony, at which each population's size will be inversely proportional to  $\gamma_i$ . The parameter  $\gamma_i$  can therefore be interpreted as the quality of the  $i$ th colony, with smaller  $\gamma_i$  corresponding to a colony of higher quality.

Previous ecological public goods models assume that the growth of each population is proportional to the average available public good (Hauert et al., 2008; Wakano et al., 2009). If we assume that the dynamics of the public good are much faster than those of the two subpopulations in system (1), i.e.,

$$\begin{aligned}\dot{u}_i &= u_i [\tilde{r}_u \phi_i - c - \gamma_i(u_i + v_i) - \mu_u] \\ \dot{v}_i &= v_i [\tilde{r}_v \phi_i - \gamma_i(u_i + v_i) - \mu_v] \\ \epsilon \dot{\phi}_i &= cu_i - [\kappa(u_i + v_i) + \delta] \phi_i\end{aligned}$$

for  $0 < \epsilon \ll 1$ , then the public good  $\phi_i$  remains close to its steady state value (Keener, 1988). In particular, for  $\epsilon \rightarrow 0$ ,  $\phi_i$  is constantly at steady state

$$\phi_i = \frac{cu_i}{\kappa(u_i + v_i) + \delta},$$

which is the average available public good. Replacing  $\phi_i$  in system (1) with the above steady state, we have

$$\begin{aligned}\dot{u}_i &= u_i \left[ \frac{r_u cu_i}{u_i + v_i + \delta} - c - \gamma_i(u_i + v_i) - \mu_u \right] \\ \dot{v}_i &= v_i \left[ \frac{r_v cu_i}{u_i + v_i + \delta} - \gamma_i(u_i + v_i) - \mu_v \right],\end{aligned}\quad (2)$$

where  $r_u = \tilde{r}_u/\kappa$ ,  $r_v = \tilde{r}_v/\kappa$ , and  $\delta = \tilde{\delta}/\kappa$ . We will assume that the dynamics of  $\phi_i$  are sufficiently fast relative to those of the two subpopulations that this approximation is valid. Moreover, system (2) is similar to the systems studied in Hauert et al. (2008) and Wakano et al. (2009), in that the growth rate of both populations is proportional to the average available public good. We therefore adopt system (2) as our model of within-colony population dynamics, and finally we define

$$\begin{aligned}F_i(u_i, v_i) &= \frac{r_u cu_i}{u_i + v_i + \delta} - c - \gamma_i(u_i + v_i) - \mu_u \\ G_i(u_i, v_i) &= \frac{r_v cu_i}{u_i + v_i + \delta} - \gamma_i(u_i + v_i) - \mu_v\end{aligned}$$

as subpopulation  $u_i$  and  $v_i$ 's respective per-capita growth rates, which we refer to as their fitnesses.

We now turn our attention to between-colony migration. In their most general form, migratory dynamics can be included in

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