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Proposal of a population dynamics model of the Public Goods Dilemma in an Ant Colony

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Abstract.This paper proposes a model of the dynamics of the public goods dilemma in an ant colony of the species *Pristomyrmex punctatus*, based on recent experimental results of Dobata and Tsuji. The proposed model, based on two predators competing for one prey, represents the interactions between the worker ant population, the cheater ant population (predators) and the public goods (prey) in the nest. The simulation results are qualitatively very similar to the experimental results obtained by Dobata and Tsuji. The model also allows the study and analysis of the long term behavior of the colony, with regard to extinction or coexistence.

Keywords. Populations Modelling, Public Goods Dilemma, Pristomyrmex Punctatus ants.

1 Introduction

There has been long-standing interest in the widespread situation in which benefits, resulting from an action by a member of a group, are private, but the costs are borne by all members of the group. In a biological context, this situation is described by saying that public goods are created by group members at some individual cost, in the expectation that cooperation will develop around them. Indeed, biologists have noticed that cooperation is frequently present in nature (see [10] and refs. therein).

However, the biologist Hardin, in a much cited paper [8], predicted that cheaters, who benefit from public goods without paying for them, will lead to the collapse of cooperation, and this is now referred to in game theory as “the tragedy of the commons” or “the public goods dilemma”. There is also experimental evidence, for interactions between viruses and cells, showing that the public goods dilemma can occur and be linked to genetic

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background. At the level of higher and more complex organisms, there has been little reported work. Dobata and Tsuji [2] provided experimental evidence for the existence of the public goods dilemma in the asexual ant species *Pristomyrmex punctatus* (henceforth *P. punctatus*), occurring between workers (cooperators) and cheaters (free riders). In this species, all workers carry out cooperative as well as asexual reproduction tasks, whereas cheaters (genetically different) reproduce themselves (i.e., cheaters) at a rate higher than the workers, without involving themselves in any cooperative tasks. In laboratory experiments, Dobata and Tsuji [2] showed that cheaters were more successful in surviving and reproducing, causing the collapse of cooperation, thus demonstrating the emergence of the public goods dilemma in a non-microbial society. Elucidation of conditions under which cooperation flourishes or collapses is an important and current topic in evolutionary biology.

This paper presents a model that reproduces the characteristics, reported by Dobata and Tsuji in [2], of the public goods dilemma in the species *P. punctatus*. The proposed model is fitted to the experimental data in [2] using the trajectory matching method, based on minimizing a sum of squared errors through the choice of model parameters. This minimization is carried out using a genetic algorithm. Since the number of parameters is quite large, a sensitivity analysis complements the fitting performed by the genetic algorithm, in order to test the model robustness as well as the parsimony of the parametrization.

2 The proposed P^3G model

The model of the *Pristomyrmex punctatus* ant species subject to the public goods dilemma proposed in this paper, which will be referred to as the P^3G model, is a modification of the model proposed in [1, 3] for two populations and one common resource or public good. One of the classes, called worker ant, is the sole producer of the resource, while the other, called cheater ant, only consumes the resource, with no contributions to its production. The proposed modifications have the objective of reproducing the characteristics reported in the experiments performed by Dobata and Tsuji [2]. It is also known from the studies of Gordon [5, 6] and [7, 9] that worker ants provide a recruitment force to produce public goods whenever they are scarce, and this fundamental characteristic of ants is also a feature of the proposed model.

The proposed model is composed of three variables, and is based on Lotka-Volterra models for competition of two predators consuming one prey, derived from the proposal of Elhanati and Schuster [3]. It consists of three coupled-nonlinear differential equations:

$$\begin{aligned} \dot{x}(t) &= F\left(y(t), z(t)\right) x(t) \\ \dot{y}(t) &= G\left(z(t)\right) y(t) \\ \dot{z}(t) &= H\left(x(t), y(t), z(t)\right) \end{aligned} \tag{1}$$

where $x(t)$, $y(t)$ and $z(t)$ are respectively, the worker ant population, the cheater ant population and the public goods, at time t. From now on we will suppose that $t \geq 0$, and t will be suppressed for brevity. The functions $F(y, z)$ and $G(z)$ represent the growth rates for each population, influenced, amongst other factors, by production and consumption of public goods in the environment. The function $H(x, y, z)$ represents the growth rate of the public goods, also affected by the production and consumption of the public goods, as well as the population densities.

The Public Goods, abbreviated to PGs from now on, represent all the goods necessary for maintenance and growth of the ant population, aggregating three main activities: nest maintenance, brood care and the search for food.

The P^3G model, is defined as:

$$\begin{aligned} \dot{x} &= \left[(b_{11} + b_{12} f(y))\, c_4 \rho_M z - (d_{11} + d_{12}\varphi(z) + d_{14} x)\right] x \\ \dot{y} &= \left[b_{21} c_5 \rho_M z - (d_{21} + d_{22} g(z))\right] y \\ \dot{z} &= c_1 \varphi(z) \rho_M^{-1} x - (c_4 x + c_5 y)\, z \end{aligned} \tag{2}$$

where b_{11} and b_{21} are the conversion rates of the public goods consumed into workers and cheaters species respectively. The term b_{12} is the workers reproduction rate in absence of cheaters in the nest. The terms d_{11} and d_{21} are the death rates by age of each ant. The terms d_{12}, d_{14} and d_{22} respectively are, the death rate by work/recruitment of the workers, the overcrowding term and the death by starvation of the cheaters. The term c_1 is the per capita production rate of the public goods, the terms c_4 and c_5 are the consumption rates of the public goods rates of each species and ρ_M is a factor of normalization.

The functions that represent the characteristics found in *P. punctatus* are: the reproduction inhibition function represented through $f(y)$, which reduces the reproduction rate of the workers with the existence of cheaters in the nest (see workers brood production reported in [2]); the starvation function, $g(z)$, increases the death rate of the cheaters when the public goods are scarce (see cheater survival data reported in [2]); and the working force function $\varphi(z)$ varies the quantity of work/recruitment of the worker ants, depending on the public goods level (refer to outside-nest adults data in [2]).

The definitions of the functions f, g, φ are as follows:

$$f(y) = \frac{1}{1 + \alpha_2 y}; \quad g(z) = \frac{1}{1 + \alpha_3 M z}; \quad \varphi(z) = 1 + g(z). \tag{3}$$

where α_2 and α_3 are factors that define the asymptotic behavior of the functions $f(y)$ and $g(z)$ respectively and M a constant, is the maximum production rate of the public goods defined in [4].

Remark: This model is scaled and normalized. The functions f,g are based on the Holling type II functions and further details on model construction as well the functions f, g and φ are given in [4]

In addition, in order to adjust the simulation results to the experimental data presented in [2], it was necessary to create an extended P^3G model, since the experimental results present the data for four populations instead of two. Thus the ODEs for the workers and cheaters were divided into two, one for the adult survivors and another for the brood production. It is important to note that, in 64 days, none of the eggs hatched. Thus there

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was no reposition in the adult population, as follows:

$$\begin{aligned} \dot{x}_1 &= \left[(b_{11,adult})c_4\rho z - (d_{11} + d_{12}\varphi(z) + d_{14}x_1)\right] x_1 \\ \dot{x}_2 &= (b_{11,offs} + b_{12}f(y))\, c_4\rho z x_1 \\ \dot{y}_1 &= \left[b_{2,adult}c_5\rho z - (d_{21} + d_{22}g(z))\right] y_1 \\ \dot{y}_2 &= b_{2,offs}c_5\rho z y_1 \\ \dot{z} &= c_1\varphi(z)\rho^{-1}x_1 - (c_4x_1 + c_5y_1)z \end{aligned} \tag{4}$$

where x_1, x_2, y_1 and y_2 respectively are, the worker adult population, the offspring of the workers, the cheater adult population and the offspring of the cheaters and z, as usual, denotes PG. The growth rates b_{11} and b_2 are divided into two growth rates, an adult rate $b_{i,adult}$ and the reproduction rate by $b_{i,offs}$.

3 Fitting the P^3G Model

In order to estimate the 15 parameters in the extended P^3G model in (4), it is necessary to first describe the behavior of the curves for $t = 64$ days reported in, the experiments of Dobata and Tsuji in [2]. Both adult populations decline, if they do not receive any reposition from the broods, while the offspring populations increase for the onset of the experiment all the broods were removed. The brood dynamics do not contain a death rate term (except for Case 4 (100% cheaters) where the eggs are neglected and all the broods die) following the short-term experimental data of Dobata-Tsuji. Using the iThink Modeling & Simulation software v9.1.4 (Isee Systems), the initial set of parameters were manually adjusted following the above specifications (for more details see [4]).

3.1 The trajectory following method using a GA optimizer

Consider:

$$\dot{\omega}(t) = \psi(\omega, p, t) \tag{5}$$

where $\omega \in \mathbb{R}^5$ is the vector state of (4), $p \in \mathbb{R}^{15}$ is the vector of parameters of the P^3G model and $\psi(\omega, p, t)$ describes the dynamics of the populations in the P^3G model. The solution of (5) is written as:

$$\omega(t) = \Psi(t, t_0, \omega, p) \tag{6}$$

A sum-of-squared errors objective function is defined as follows:

$$E(p) = \sum_{i=0}^{4} \left[\Omega^i_{DT} - \Psi(64, 0, \omega^i_0, p)\right]^2 \tag{7}$$

where $E(p)$ represents the objective function dependent on p to be minimized, Ω^i_{DT} are the means of experimental results in [2] after 64 days and $\Psi(\cdot)$ are the results of the model given in (6) for the five cases with $i = 0, ..., 4$.

$E(p)$ was minimized with the standard genetic algorithm tool GA, in MatLab R2011a (GA Revision 1.1.6.6, 2010/11/08), employing the Stochastic Uniform selection function

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and lower bounds of 0 for all parameters, to ensure their nonnegativity. The initial population was that of manually adjusted parameters, see above. The GA was run 20 times and the best scoring result was selected. Then the parameters d_{14}, c_1, c_4, c_5 and α_3 were frozen as shown in Table 1, the GA was run 20 times again with the parameters frozen and the best scoring set of resulting parameters was selected as shown in Table 1 (see details about the procedure in [4]).

Table 1: Estimated values for the parameters in the P^3G model. *Frozen parameters

Parameter	b_{11}	b_{12}	d_{11}	d_{12}	$d_{14}*$	b_{21}	d_{12}	d_{22}
Value	0.0147	0.0066	0.0119	0.0207	0.001	0.0442	0.0009	0.0242
Parameter		c_1*	c_4*	c_5*	α_2	α_3*		
value		1.8	21	10	500.01	3		

4 Results

Using the estimated parameters, the simulated results and the average of the experimental results were plotted in order to verify the quality of the fit with respect to the experimental data presented by Dobata and Tsuji [2], (see figure 1).

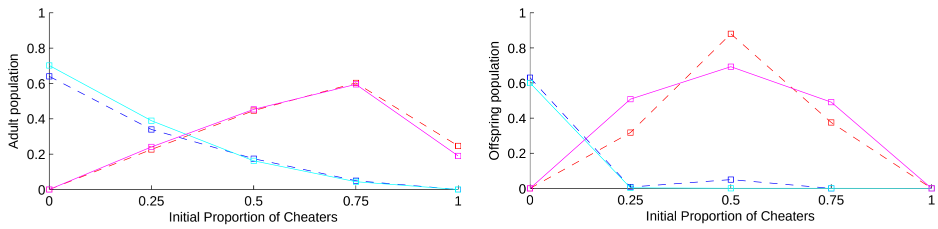

Figure 1: Comparison between the simulation results and the experimental data for both the workers and cheaters species. A:Proportion of surviving adults, B: Offspring produced. Blue curve: workers experimental data, cyan curve: workers simulation results, red curve: cheaters experimental data, pink curve: cheaters simulation results.

Figure 1 shows that the results of the simulations fit well to the experimental results and follow the behavior in the five cases, for the results after 64 days of the experiment. Then, returning to the P^3G model in (2) and with the parameters shown in the Table 1, the dynamics of the model during 64 days were plotted (Figure 2).

Finally, in order to determine the robustness of the parameters estimated, the span of variation of parameters that kept the dynamics within the experimental range (meaning the matching between the 64-day simulations and the measured data) was assessed. Large allowable variation in a parameter corresponds to a low sensitivity of the model to the parameter. Details of this analysis are explained in [4], and the results obtained are shown in Table 2.

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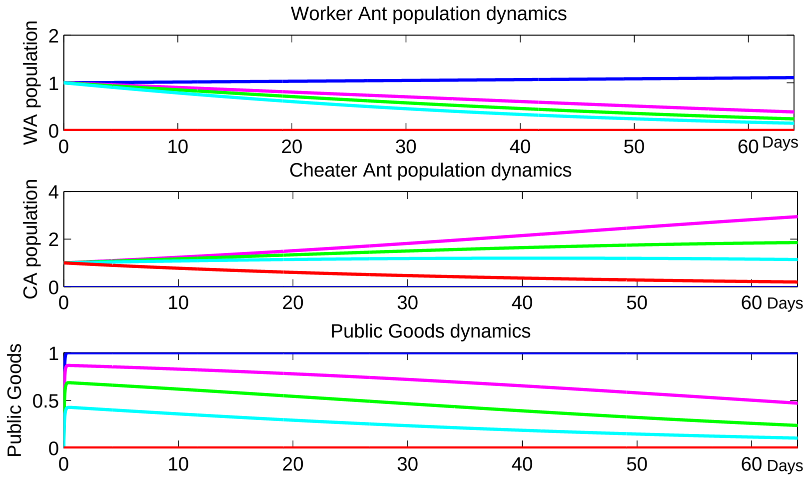

Figure 2: Simulation for the worker population, cheater population and Public Goods in five cases format. Blue: Case 0, Pink: Case 1, Green: Case 2, Cyan: Case 3 and Red: Case 4.

Table 2: Allowed variation of the parameters respect to the dynamics of Dobata and Tsuji.

Responsive				Insensitive			
c_1	9%	b_2	11%	d_{21}	38%	d_{11}	41%
c_4	12%	c_5	14%	b_{12}	54%	d_{22}	69%
b_{11}	19%	d_{12}	24%	α_2	91%	α_3	91%

These sensibility results show that there exist two sets of parameters whose variation affects, to a greater or lesser extent, the end result of the simulations, the most sensitive parameter being c_1. The most sensitive parameter may vary by 9% of before simulated results fall outside the range of the experimental results.

5 Conclusions

Noting that the P^3G model was fitted to a sparse quantity of experimental data, it successfully reproduced the qualitative behavior, and the characteristics (the recruitment/work force, the inhibition of reproduction of the workers in presence of cheaters, etc), presented in the results of the experiments of Dobata and Tsuji in [2].

Moreover, the simulations of the P^3G model along the 64 days show that the model could reproduce the dynamics of the public goods dilemma (see Figure 2), where the colonies in the presence of cheater ants present a behavior of extinction of the worker population even with the broods in the count (recalling in the model in (2) the worker population are constituted by the adult ants and the broods.). With the decrement of the worker class, the production of the PGs also decreases, leading to the extinction of the

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colony, as predicted by [11].

As explained by [12] only when the population is solely composed by worker ants can the colony persist, in which case the population also grows with time.

The sensitivity analysis also suggests that the model, together with the estimated parameters, is robust, since the dynamics is maintained even for changes of up to 9% in the parameters. The proposed model, if validated by more experimental results, may result in a tool for the specialists (e.g. myrmecologists) in the analysis of the behaviour of the *Pristomyrmex punctatus*.

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