

Artificial Life, Examining Levels of Cooperation between Simulated Insects Dependant on Relatedness Measures

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ABSTRACT

Cooperative behaviour can be found in many insect societies. A form of this cooperation known as Eusociality is only found in 2% of known insect species, however, these species compose most of the world's insect biomass. This study investigated the origins of cooperation in eusocial species by analysing the effects of individual relatedness and patch richness on the levels of cooperation observed. These results allowed commentary on the validity of the game theoretic model by Reeve and Hölldobler and provided insight into the origins of cooperation. A custom Agent Based System (ABS) simulation was developed, with results providing insight into multiple aspects leading to the evolution of cooperation. By comparing the results to Reeve and Hölldobler's game theoretic model, the study was able to agree with two of the organizational trends (hypotheses) they mentioned, indicating that higher levels of agent relatedness and higher levels of patch richness (resource density) both lead to higher levels of within-group cooperation.

The study was therefore able to comment on the origins of cooperation in biological societies and proved that relatedness has a strong effect on the cooperation experienced.

Finally it would be possible to extend this method of study to address the other hypotheses mentioned by Reeve and Hölldobler.

CCS Concepts

•Computing methodologies → Machine learning; Artificial intelligence; *Distributed artificial intelligence; Machine learning approaches; Bio-inspired approaches*; Multi-agent systems; Cooperation and coordination; Neural networks; Artificial life; Genetic algorithms;

Keywords

Machine Learning, Artificial Intelligence, Artificial Life, Agent Based Systems, Eusociality

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PLDI '13 June 16–19, 2013, Seattle, WA, USA

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DOI: 10.475/123.4

1. INTRODUCTION

Cooperative behaviour can be found in many insect societies [23, 47, 59, 51, 60], however, a form of this cooperation known as Eusociality is only found in 2% of known insect species [59]. These species compose most of the insect biomass [59, 23]. As documented by Wilson and Hölldobler [60], better organized groups outperform reclusive individuals in resource competition, while larger groups outperform those of the same species. The large survival advantage given by cooperation is the reason for these disproportionate results. Although the evolution of cooperative behaviour is not common, it is proven to be advantageous to the long term survival of a species [60], and its origins are therefore worth further study.

Agent-Based Systems (ABS) [17] are a subset of Artificial Intelligence (AI) [45]. ABS are made up of intelligent agents [61], which are autonomous systems able to observe and act within an environment. Various studies have been conducted around the design of effective agent controllers within ABS [62, 61, 17, 54, 10]. This has often proved to be a difficult task, as the agents' actions depend not only on feedback from the environment, but also on the actions of other agents. Evolutionary Computation (EC) [16] and Neuro-Evolution (NE) [31] have been suggested as effective methods to create novel and effective agent controllers within ABS. NE makes use of a subset of EC to create and adapt agents' controllers and has been shown to achieve high performance in many tasks, for example in the fields of automated robotic controller design [53], artificially capturing of human creative expression [15] and agents learning to play different video games [21].

This study will attempt to comment on the validity of two of the organizational trends stated by Reeve and Hölldobler [44]. Namely, 1) that higher levels of within-group agent relatedness lead to higher levels of within-group cooperation and 2) that as patch richness increases, both colony size and the number of competing colonies increases, leading to higher levels of within-group cooperation. To achieve this, this study will make use of an ABS simulation based on the concept of Artificial Life (ALife) [27] which aims to investigate the origins of social aspects within the context of computer simulations.

The main research areas include the cooperation and competition found in biological systems and how these may be represented and studied by making use of an ABS simulation. The following background information serves the purpose of reviewing relevant literature within the fields of

Social Insects, Agent-Based Models (ABM), Artificial Life (ALife) and Multi-agent cooperative and competitive behaviour. These areas will be discussed in their respective order, with methodology to follow. Finally findings and results will be discussed with conclusions drawn.

1.1 Research Objectives

The following research objectives (linked to the organizational trends stated by Reeve and Hölldobler [44]) serve to highlight the research objectives of this study:

The primary objective is to determine if the more genetically related members of a group are, the more likely they will behave cooperatively towards each other. From this the following hypothesis was tested.

H1: Higher levels of between-group agent relatedness lead to higher levels of within-group cooperation between agents.

The secondary objective is to determine if higher levels of patch richness lead to the development of higher cooperation between members of a group. From this the following hypothesis was tested.

H2: Higher levels of patch richness (resource density per patch) leads to larger group sizes and more competing groups and therefore a higher degree of within-group cooperation.

2. SOCIAL INSECTS

Eusociality is a prime example of cooperative behaviour as it depicts members putting the betterment of the group over themselves. Kin selection is one of the prevailing theories to explain the emergence of eusocial behaviour and therefore cooperation in insect societies.

2.1 Hamilton's Kin Selection Theory

Past studies have examined eusociality and its origins, with a field known as "kin theory" emerging as a popular explanation [20, 19]. Kin theory also known as "Hamilton's Rule" [20, 19] states that the more genetically related members in a group are, the more likely they are to behave altruistically towards each other [59].

Nowak *et al.* [39] argued that this theory is rather a consequence of eusociality as opposed to a cause of it. The point has been further addressed in the study by Wilson [59], where alternative conditions for the evolution of eusociality were addressed. An example of an alternative condition, is known as group selection, which tends to favour greater genetic variability and result in lower levels of relatedness [59]. This example results in high levels of within-group cooperation where agents may experience a greater fitness than they would with higher kinship.

Reeve and Hölldobler [44] attempted to provide an explanation for the cooperation found in insect societies by making use of an individual selection model mediated by between group-competition. After surveys of insect societies they found 4 recurring organizational trends. The first trend describes that the highest levels of cooperation (and therefore altruism) are found amongst closely related groups [44]. This point closely mimics Hamilton's kin selection theory and is the main focus of this study.

2.2 Game Theoretic Agent Based Model

Reeve and Hölldobler [44] continued to develop a mathematical game-theoretic model which made use of tug-of-war

theory [44, 48, 34]. This model represented mutual policing which is defined by agents working to increase both their own share of resources (and therefore fitness) while at the same time decreasing that of others. This behaviour occurs both within and between-groups.

The model attempted to describe the various interactions between cooperation and competition within a species in order to determine the origins of cooperation and "super-organismness". Where a "superorganism" [44, 58, 47, 9] is defined as a group of agents that act collectively to produce behaviour which is advantageous to the group. Individuals in such a system exhibit elaborate levels of cooperation and are not able to survive without their group.

By analysing derivatives of their model, Reeve and Hölldobler were able to identify 4 factors which are responsible for the increase of within-group cooperation. Specifically within-group cooperation increases as (i) group size decreases, (ii) the number of competing groups increases, (iii) the within-group relatedness increases (group diversity decreases) and (iv) the between-group relatedness decreases (population diversity increases). These factors create the basis of the organizational trends and their accuracy will need to be analysed.

Although Reeve and Hölldobler believed genetic relatedness to be an important factor to the rise of within-group cooperation, they do state that while their model does predict that relatedness is found before the occurrence of within-group cooperation, it is not the only necessity for its existence.

They continue to provide an example of an alternative case where cooperation may exist in nearly unrelated individuals of a "super-colony" which arises from the effect of between-group competition. A possible explanation for this level of between-group competition is a large number of competition groups, which creates competition in an environment and in turn will cause higher levels of within-group cooperation.

Multiple studies of different kinds of collective gathering tasks have been taken [30, 46, 42], ranging from Artificial Life (ALife) [27], to Multi-Agent Systems (MAS). They are typically based upon observations of social insects and are used as a means to study different levels of cooperation which emerge in such simulated agents.

While Reeve and Hölldobler's model is a promising approach to explain the 4 organizational trends found, its accuracy must still be tested. The formal testing required is difficult to perform in a biological system which leads to the advantage of using a simulation environment. Therefore an ABS would be well suited to this biologically based model and would allow novel testing to be completed.

3. AGENT BASED SYSTEMS (ABS) AND ARTIFICIAL LIFE (ALIFE)

Artificial life (ALife) [28] is a research field aiming to investigate multiple disciplines, namely the origins of life, evolution, learning and more [57, 6, 1]. It does so by simulating multiple generations of open-ended evolving digital organisms. It is therefore the study of artificial systems which exhibit behaviours normally attributed with natural systems [27].

This area's aim is to develop a theory of life in all of its forms, and has potential applications in multiple areas, from the creation of new forms of artificial life, to the study

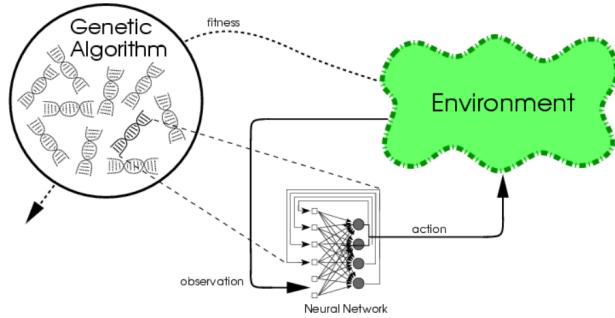


Figure 1: Neuro-Evolution (NE) Process [31]

of new forms of evolvable drugs, hardware and prosthetics with many more possibilities [6]. ALife makes use of biologically inspired approaches such as artificial evolution and unsupervised learning to control the organisms actions within simulated environments.

Agent Based Systems (ABS) [29] are a subset of Artificial Intelligence (AI), AI similarly to ALife, is the study of artificial systems which exhibit behaviours normally attributed with natural intelligence [27].

Such systems consist of multiple agents which are problem solving entities situated in a specific environment with strict design objectives. These agents are capable of flexible and autonomous control over their internal state and behaviour [62].

While possibly disadvantageous in software development techniques due to emergent behaviour [62], ABS have been used many times to represent experiments which are difficult to perform, and have been applied to various disciplines for example, biology, anthropology and medicine [7, 2, 36].

In biological systems it is often difficult to observe and measure aspects of a species over many generations. ABS's main use is to test hypotheses in situations where they would normally be difficult to test. Another advantage of ABS in biological systems was spoken about by Bonabeau [8] where he provides an example that "it is more natural to describe how shoppers move in a supermarket than to come up with the equations that govern the dynamics of the density of shoppers". This fact is mimicked in biological systems where it is more natural to describe the biological behaviours and simulate the results, as opposed to designing equations to analyse the effects of the behaviour.

While ABS provide many benefits to biological systems there are also issues that need to be looked at. Specifically ABS need to represent a model with the right amount of detail, creating this can prove to be difficult. ABS also have the possibility to become computationally expensive thus requiring large simulation time for certain models.

The form of ALife in review consists of ABSs. Within

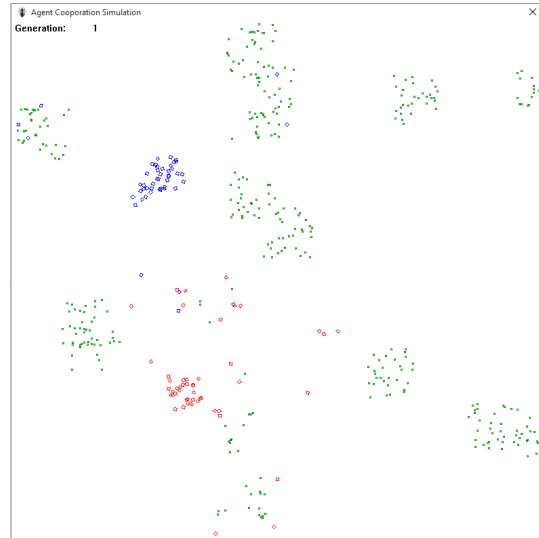


Figure 2: ABS Framework with the inclusion of agent groups represented in red and blue and resource objects represented in green.

this form reactive agents are found. While it has historically been difficult to demonstrate advantageous emergent behaviour in such systems due to the possibility for undesirable learned behaviours, such a system is also a good example of how collectively intelligent systems may be generated from simple agents [37]. This factor plays an important role in the use of ABS within this study where within-group cooperation is seen as an emergent behaviour that may naturally occur from such a system [8].

4. CONTROLLER DESIGN AND AGENT BEHAVIOUR IN AGENT BASED MODELS

Automated controller design [18, 55] is a process used to create novel agent controllers without the need for human interaction. Controllers are responsible for the actions of agents within an environment, and must be designed to be able to perform as best as possible for the task at hand (for example, resource foraging, reproduction, collaborative box pushing). Although it is possible for these to be designed by hand (known as heuristic controllers), these are limited as they cannot anticipate all possible situations in complex environments.

4.1 Machine Learning (ML)

Machine Learning (ML) is a subfield of AI responsible for the design and analysis of algorithms which are able to learn from their experience in an environment and improve their performance at specific tasks [32, 13]. ML makes use of multiple types of learning namely, Supervised, Unsupervised and Reward-based learning [45], all providing different benefits and are chosen based on the different forms of feedback given by the environment.

By making use of ML techniques, it is possible to create novel agent controllers, which are correctly suited for specific environments. In Unsupervised Learning no feedback is provided. This method is used when we need to be able to make predictions for unseen data for which we are never provided training examples. Examples of unsupervised learning

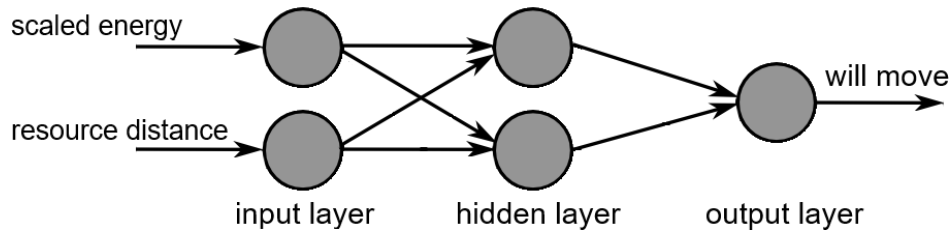


Figure 3: Architecture of the agent controller defined by a fully connected multi-layer neural network

approaches can be found in Self Organising Maps (SOMs) [26], Neuro-Evolution (NE) [31] and more. Where, as shown by [53, 52, 15] its applications range from automated robotic controller design, and Intrusion Detection Systems (IDSs) to artificially capturing human creative expression. Evolutionary Computation (EC) [42] is a type of unsupervised learning and falls under the field of directed random (stochastic) search methods.

Finally the type of learning considered for this study makes use of NE techniques further described in the experimental design chapter. Such approaches make use of EC methods to evolve learned individual and emergent global behaviours within our ABS.

4.2 Neuro-Evolution (NE)

Neuro-Evolution (NE) [31] is the adaptation of Artificial Neural Networks (ANNs) using Evolutionary Algorithms (EAs) and follows the process as detailed by figure 1. NE is used to adapt the weights of an ANN until an optimal configuration is found. It does so by using an EA to search for specific network configurations within a set of candidate solutions by crossing over and mutating agent ANNs, finally producing adapted offspring. The weights control agent’s behaviour [41], and therefore as these weights are adapted the agent’s behaviour is refined. This process results in the autonomous creation and evolution of agent controllers. Due to the use of the EAs, NE is helpful to use in situations where we do not know correct training examples and acts as a form of unsupervised learning.

4.2.1 Evolutionary Computation (EC)

Evolutionary Computation (EC) aims to mimic the evolutionary processes of nature. An agent’s controller, is evolved in order to maximise potential reward without seeking to estimate a specific value function. Many researchers have demonstrated EC to be an effective method for agent controller design [5, 38].

4.2.2 Evolutionary Algorithms (EAs)

EAs are a subset of EC and are a class of population based stochastic search algorithms based on the concepts of Darwinian Evolution [63]. EAs are useful when dealing with large problems, because they are less likely to be trapped in local optima and are able to function in situations where little information is known.

4.2.3 Artificial Neural Network (ANN)

Artificial Neural Networks (ANNs) [41] form an integral part of the NE process. ANNs are based on the biology of the brain, where the interconnected nodes making up the ANN can be compared to the interconnected neurons of the brain [32]. The links between the nodes in the ANN can

be thought of as synapses. ANNs have been used in multiple studies and are able to provide a robust approach to approximating functions. As shown by Cybenko [14] a fully-connected neural network with a single hidden layer is Universal Function Approximator, and is able to approximate any continuous function.

5. EXPERIMENTAL METHOD

The experimental setup consisted of a 20cm by 20cm sized continuous environment where agents were able to move freely, collect resources and form groups (analogous to colonies in real world insect societies) [35]. The goal of the simulation was to study the origins of cooperation in simulated insect societies. The experiment allowed us to comment on the validity of Reeve and Hölldobler’s [44] hypotheses stating that the highest levels of altruism are found amongst closely related groups, and that higher levels of patch richness lead to higher levels of within-group cooperation.

To create the necessity for cooperation, a foraging task in the form of resource collection was chosen.

Results for cooperation and diversity of agents were taken based on variations of a parameter known as the Relatedness Threshold (RT) value, which indicated how closely related agents were required to be to fall under the same group.

The ALife simulation was run multiple times for each RT value, each of these runs spanned many generations with average results taken. Simulation runs were conducted on multiple environments consisting of many agents and different resource distributions. Each run began with the same agent and resource configuration (resource configurations were specific to each environment), which were loaded from an initialisation file.

5.1 Agent Based Model

To represent the agent based framework we made use of a custom designed agent-based system ¹. An example of this system is presented in figure 2 which depicts 2 agent groups within a specific environment configuration. The simulation included agents, groups, resources, environmental configuration and generations (the lifetime of a single agent).

Although Reeve and Hölldobler [44] did not have a strict definition of cooperation they did represent a value known as the “selfish fraction” which was the fraction of an agent’s energy that was spent selfishly. We extended this definition to define within-group cooperation as the percentage of agents within a group that acted cooperatively (defined as an agent collecting at least a single resource for the group) towards their group. Between-group cooperation refers to

¹The custom Agent Based Framework can be found at <https://bitbucket.org/ZMel/poseidon>

Table 1: Experimental Specific Parameters

Environmental Parameter Settings				
	Experiment 1	Experiment 2	Experiment 3	Experiment 4
Number of patches	1	1	5	5
Number of Resources	600	900	600	900
Resource Distribution	Uniform Distribution	Uniform Distribution	Patchy Distribution	Patchy Distribution
Relatedness Threshold	0.0 - 1.0 steps of 1/6	0.0 - 1.0 steps of 1/6	0.0 - 1.0 steps of 1/6	0.5
Experiment Test	Impact of Relatedness on Within-group Cooperation	Impact of Less Resource Competition on Within-group Cooperation	Impact of Higher Competition Resource Distributions on Within-group Cooperation	Impact of Higher Patch Richness on Within-group Cooperation

the percentage of groups that are cooperative to one another, in the current generation. A groups between-group cooperation value, is calculated by determining the percentage of groups that consume within their share of resources in the generation (each groups share of resources is calculated based on the number of agents in the group).

5.2 Population and Genetic Architecture

The population in question consisted of 100 agents each with a randomly generated ANN architecture, making use of a Cauchy Distribution for weight initialisation. The ANN held a one to one mapping [63] where the genotype and consisted of a vector of floating point values which represented the ANN weights. This population resulted in an initial within-group cooperation value of 50% which was ideal for testing conditions because agents were not predisposed to either cooperative or competitive behaviour. Agents would then be able to evolve based on the environment and parameters in use. The agent population was saved to file and reloaded in each test to allow consistency between different test runs.

The ANN required a design that was able to represent both cooperative and selfish behaviour and thus the inputs needed to be carefully chosen. Agents were controlled by a feed-forward ANN [63, 64, 22, 50] with two inputs, a single layer of two hidden nodes and a single output value. A sigmoid activation function was used to define node output. The agent's inputs consisted of a scaled value of both the agent's current energy and the squared distance between the agent and its closest resource.

Based on this input the agents' ANN output value would determine how they would like to act within the environment and foraging task at hand. If they would like to remain selfish and not move in order to conserve energy, or rather expend energy and attempt to retrieve the closest resource and be cooperative towards their group. ANN weight values were constrained between the range of $[-1, 1]$ as was its input.

The ANN design resulted in a range of robust behaviours, namely agents that were completely cooperative or competitive towards their groups and others whose behaviour alternated between the two. An example of this was observed in certain agents that would move when the environment was resource rich but stop moving as resources were consumed. After more resources grew the agents would begin to move. This indicated the effectiveness of this design which allowed

a varying range of agent behaviour.

5.3 Foraging Task

Resource collection has been used in many different studies [56, 30, 46, 42], has many real world applications and occurs naturally in many insect societies. This task also provides a means for evolution of the system as well as the definitions for cooperation provided.

Each agent gains energy in the environment by resource collection. The agents make use of their energy to move in the environment, with the movement cost per tick and energy gained per resources detailed in table 2.

The foraging task is defined as individual foraging [56]. Once collected, the energy from a resource could be used to move and collect new resources or rather act selfishly in order to store energy by not moving. Any collected energy at the end of a generation is pooled together by a groups constituent agents and forms the groups energy for the next generation.

Resources are allocated a specific regrow rate (indicating after how many simulation ticks a new resource should grow) which is detailed in table 2. The regrow rate had to be low enough to allow a sufficient environmental carrying capacity [43] for each environment and also high enough to include a sufficient amount of competition which is required for the evolution of cooperation.

Specific environment configurations are detailed in table 1. The environments allowed the levels of competition to be altered. The level of competition in the first environment is used as a base or middle ground, with the second environment representing the lowest level of competition and the third representing the highest. A fourth environment was included in order to aid the testing of the second hypothesis of this study, this environment made use of the same resource distribution as the third but increased the patch richness by 50%.

The individual nature of this task means that no specific cooperation is needed for its completion, while cooperation is not directly necessary, it does evolve as a consequence of resource collection [44]. This is found because the specific resource configuration accounts for a certain carrying capacity of the environment. The carrying capacity causes a certain level of competition between agents and groups, and in antithesis to this a certain level of cooperation will develop between the population and agents within specific

Figure 4: Custom EA Pseudocode

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1. Join and sort the agents based on their energy (Fitness);
2. While we do not have n pairs of parents
3. REPEAT
  (a) While we do not have a pair of parents
  (b) REPEAT
    - Use rank based selection to select the first parent;
    - Use rank based selection to select the second parent;
    - If the second parent is different to the first
      * Add the pair of parents;
  (c) For all n pairs of parents
    - Choose a random percentage selection chance between 0 and 1;
    - If the selection chance is <= the relatedness between the pair;
    - Create 4 children from pair
    - REPEAT
      * Create child by crossing over parent ANNs using a single point crossover;
      * Possibly mutate child ANN;
      * Split children into groups;

```

Table 2: Simulation Parameter Settings

Simulation Parameter Settings	
	Value
Number of Inputs	2
Number of Hidden Neurons	2
Number of Output Neurons	1
Number of Hidden Layers	1
Maximum Turn Rate	0.9
Maximum Movement Speed	1.0
Agent Lifetime (No Generations)	1
Number of Initial Agents	100
Number of Initial Groups	1
FOV (Field of View) Radius	2000
Energy Gained Per Resource	20
Movement Energy Cost Per Tick	0.2
Group Starting Energy	20000
Crossover Rate	1.0
Crossover Operator	Single Point
Mutation Rate	0.1
Rank Based Selection Pressure	1.5
Number of Children Per Parent Pair	4
Maximum Mutation Perturbation	0.1
Relatedness Threshold Value	0.0 - 1.0 steps of 1/6
Maximum Gene Distance	0.01
Generations Per Simulation Run	50
Number of Simulation Runs	20
Resource Regrowth Rate (Regrow every x ticks of inactivity)	500

groups.

5.4 Experimental Design

Results of the ALife simulation were taken based on variations of the RT parameter within the range detailed in t

Each simulation run began by initialising the system parameter settings, initial agent configuration and specific resource distribution from an initialization file. Initially the system was designed to randomly generate a new agent and environmental configuration each time it was run. The initialization file was a necessary adaptation that allowed consistency between experiments and introduced a simple av-

enue for statistical analysis. Four environments were tested, each representing a different experiment, with details of each experiment found in table 1.

5.4.1 Parameter Settings

Multiple pre-tests on the system were completed during its development, with results recorded in order to choose parameter values for the final experiment. With the final values for these parameters depicted in table 2.

On the completion of a generation the custom EA followed the pseudocode represented in figure 4 and made use of a rank based selection technique [4, 3] to choose multiple par-

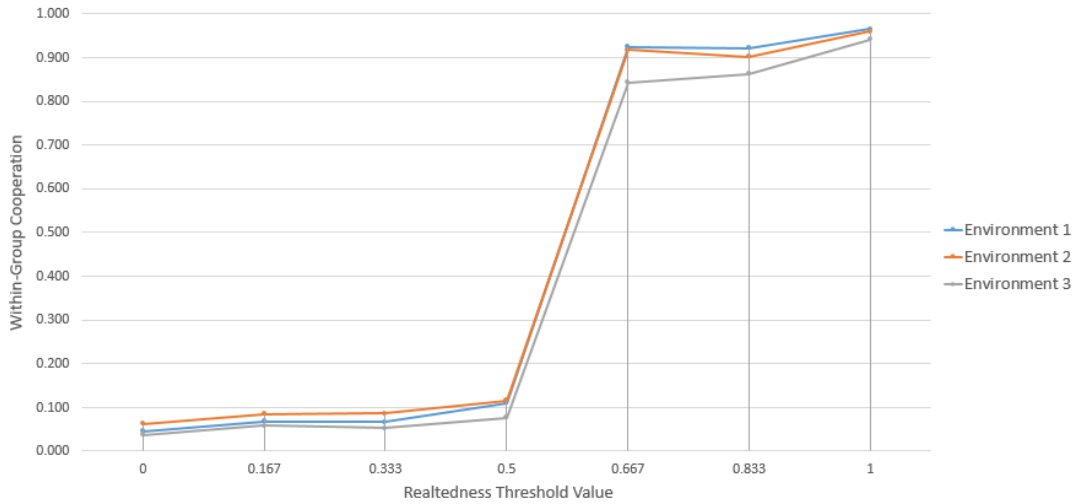


Figure 5: Graph Displaying the Degree of Within-Group Cooperation Experienced Per Tested Environment at Each Relatedness Threshold Value

ents which were responsible for repopulating the next generation. To determine whether or not two agents were compatible for reproduction, a relatedness measure was used. This measure is composed of a Hamming distance function [33] with respect to agent ANNs. The parents compatibility defined a percentage chance of whether or not they would reproduce.

Children were placed into different groups based on their relatedness to the group as well as the current RT value. The children would replace the parent population and become the population for the next generation.

During each generation snapshots of the entire experiment were recorded, allowing both a per generation and per simulation statistical record to be established.

Values of within-group and between-group cooperation, group and population diversity, the average number of groups formed and the average number of agents per group, per generation were recorded. Using an evaluation programme, the snapshots for each experiment were analysed with results averaged over 50 generations per run and 20 runs per experiment. Although running the simulation for more generations and runs would have been beneficial, due to the expensive nature of the simulation this was not possible. The number of generations and runs were chosen after a stabilisation of results were found.

Finally results were tabulated and statistical analyses were performed to comment on the validity of the hypotheses of this study.

6. RESULTS AND DISCUSSION

The experiment followed the process as detailed in the Experimental Design section of this paper. Multiple analyses of the system were completed over many environments in order to test the effect that RT values and patch richness have on the levels of within-group cooperation experienced. Each simulation environment represented a different resource configuration and allowed the concurrent analysis of the hypotheses of this paper. From the results obtained conclusions were drawn and compared to the organizational trends and factors discovered by Reeve and Hölldobler which

play an effect on the increase of within-group cooperation.

6.1 Results

As can be seen from the results presented in graph 5 and tables 3, 4, 5, there is a positive relationship between the RT and the within-group cooperation values experienced, with consistent behaviour across environments.

Statistical analyses were performed on the results obtained from the environments mentioned above.² To perform the analyses, first a Kolmogorov-Smirnov (KS-test) [25] test was conducted to test for normality of data. The data was not found to be consistent with a normal distribution and so the non-parametric KS-test was used to test for statistical significance between results.

In the case of the first hypothesis a Bonferroni-Correction [12] was performed altering the significance level α for each KS-test to maintain accuracy of results. The within-group cooperation results for each RT value were compared with the results from each other RT value, this process was repeated across all environments. It was found that the within-group cooperation results obtained per environment were seen to be statistically significant across all RT values with few exceptions.

The second hypothesis involved altering the level of patch richness and measuring the change in within-group cooperation that occurred while keeping the RT value constant. To perform this test environments 1 and 3 were used as baselines, two new environments (2 and 4) were then created by increasing the patch richness of 1 and 3 by 50%. This allowed us to determine if an increase in patch richness has an effect on the levels of within-group cooperation experienced. A KS-test was used between environments 1 and 2, and, 3 and 4. From these tests it was found that the level of patch richness plays a significant effect on within-group cooperation. It was also found that this will only occur if there is sufficient competition in the base environment for the change in richness to have an effect on the cooperation

²All simulation results data (and supporting statistical tests) can be found online at <http://poseidonthonours.github.io/relatedness.html>

Table 3: Statistical Results of Experiment 1, Testing the Impact of Relatedness on Within-group Cooperation

Environment 1 Results, Correlations and Stable Ranges						
Relatedness Threshold	Within-group Cooperation	Between-group Cooperation	No Groups Formed	No Agents Per Group	Group Diversity	Population Diversity
0.0	0.046	1	1	6131.390	0.640	0.640
0.167	0.068	0.452	2.933	3183.010	0.561	0.598
0.333	0.067	0.463	2.702	3314.190	0.559	0.592
0.5	0.111	0.202	7.865	886.969	0.458	0.562
0.667	0.924	0.123	25.817	4.738	0.060	0.584
0.833	0.922	0.117	25.970	4.661	0.060	0.584
1.0	0.965	0.107	34.923	3.424	0.012	0.577
Mean	0.443	0.352	14.459	1932.626	0.336	0.591
SD	0.462	0.325	14.000	2357.641	0.278	0.024
Correlation 1	-0.964					
Correlation 2	0.964					
Correlation 3	-0.964					
Correlation 4	-0.750					
Stable Range 1	From 0.167 to 0.333 no significant difference was found with a P-Value = 0.771 and $\alpha = 0.010$					
Stable Range 2	From 0.667 to 0.833 no significant difference was found with a P-Value = 0.497 and $\alpha = 0.025$					

Table 4: Statistical Results of Experiment 2, Testing the Impact of Less Between-group Competition on Within-group Cooperation

Environment 2 Results, Correlations and Stable Ranges						
Relatedness Threshold	Within-group Cooperation	Between-group Cooperation	No Groups Formed	No Agents Per Group	Group Diversity	Population Diversity
0	0.062	1	1	10738.500	0.639	0.639
0.167	0.085	0.335	3.222	6149.060	0.564	0.596
0.333	0.086	0.339	3.119	6530.110	0.565	0.601
0.5	0.116	0.062	9.732	1547.860	0.475	0.560
0.667	0.917	0.089	46.245	5.019	0.061	0.610
0.833	0.901	0.087	45.744	5.571	0.064	0.596
1	0.960	0.066	62.532	3.805	0.012	0.609
Mean	0.447	0.282	24.513	3568.561	0.340	0.602
SD	0.449	0.340	25.983	4262.672	0.280	0.024
Correlation 1	-0.964					
Correlation 2	0.964					
Correlation 3	-0.964					
Correlation 4	0.036					
Stable Range 1	From 0.167 to 0.333 no significant difference was found with a P-Value = 0.771 and $\alpha = 0.010$					
Stable Range 2	From 0.667 to 0.833 no significant difference was found with a P-Value = 0.771 and $\alpha = 0.025$					

found.

Finally a Spearman rank correlation [66, 65] measure was used to test the validity of the 4 factors discussed. The within-group cooperation was therefore compared with, the average number of groups formed (Correlation 1), the average number of agents per group (Correlation 2), the average group diversity (Correlation 3), and the average population diversity experienced (Correlation 4).

Statistical results for these tests are presented in tables 3, 4 and 5.

6.2 Discussion

This study tested the validity of two of the organizational trends and the game theoretic model by Reeve and Hölldobler [44], while also commenting on the origins of cooper-

ation as well as factors leading to its increase.

In order to determine if RT have a significant effect on levels of within-group cooperation, statistical analyses comparing results between RT values were performed. From the analyses it was found that there is a significant difference between the amount of within-group cooperation experienced for each RT value, tested using α significance levels calculated by the Bonferroni-Correction method.

While it was found that the RT value caused a significant difference in the levels within-group cooperation, there were specific cases in each environment where the values obtained from one RT value were not significantly different from the previous. Such cases can be defined as "stable ranges" and are depicted in tables 3, 4 and 5.

A possible reason for these insignificant results is due to

the effect that each RT value has on the carrying capacity of an environment. If different RT values create very similar carrying capacities, the number of groups formed in each environment will be similar, which causes similar levels of competition and therefore within-group cooperation.

In order to determine if the RT value holds its effect across multiple environments (which include different resource configurations and therefore carrying capacities) a KS-test was used to compare results between different environments.

By analysing the results of a KS-test with a significance level α of 0.05, on the results between environments 1 and 2, it was found that insignificant differences occurred in the resultant P-values, within the larger range of RT values (≥ 0.5). Significant differences were found in the lower range (< 0.5), where more within-group cooperation was found. These results show that the change between environments (change in resource distribution by increasing patch richness) has less effect on the cooperation experienced than the RT does. We can see this by observing that as the RT value increases so does the selection pressure and the level of competition. In this case, there is no significant difference between the results in either environment and therefore the RT value has a greater effect on the results obtained than the increase in patch richness.

By analysing the results of a KS-test with a significance level α of 0.05, on the results between environments 1 and 3, it was found that insignificant differences occurred in the resultant P-values, within the lower range of RT values. Specifically found at values 0.167 and 0.333. These results show that it is likely that the change in environment (change in the resource distribution by increasing the number of patches) has a comparable or larger effect on the cooperation than the RT values do. If the environment had little to no effect, we would expect to see no significant difference in all cases, however, the effect of the RT value is not enough to overpower the effect created by the change in environments.

If we look at the average values obtained in tables 3 and 5, we can also see that the levels of within-group cooperation are higher for the first environment than the third for all RT values. It is therefore possible that the change in environments (from low competition to high competition) has a larger effect on the results obtained than the RT value has. This indicates that the level of competition in an environment plays a strong effect on the results obtained.

From these analyses we were able to confirm that RT values play an important role in the level within-group cooperation experienced. We were able to observe that the ABS simulation agreed with the first organizational trend mentioned by Reeve and Hölldobler and were able to accept *H1*, stating that "the most elaborated cooperation occurs in groups of relatives" and finally reject the null hypothesis for this case. Within-group cooperation was found to increase due to the levels of relatedness and were therefore not simply a result of eusociality, which goes against the argument by Nowak *et al.* [39].

While we found that RT values have a large effect on the levels of within-group cooperation, it was also seen that the environmental configuration has a strong effect. In order to analyse the effect of environmental configurations, the concept of patch richness was used as a test measure. As can be seen in table 6, while the number of patches is kept constant and patch richness is increased, an increase in the

number of competition groups, number of agents per group and within-group cooperation is found.

In order to determine if these results were statistically significant a KS-test was performed on the levels of within-group cooperation obtained within each environment. The α was chosen at a significance level of 0.05.

It was found that the difference between values for environment 1 and 2 were not statistically significant with a P-Value of 0.135. A possible reason for this is that the uniform configuration consisting of a single patch plays more of an effect on the level of competition than the level of patch richness does. In other words the environment with a uniform distribution is more favourable to agents because there is less competition and agents do not need to explore as much, in order to find resources. This means that the environments level of competition is already low enough that an increase in richness has little effect on the results obtained.

While the second and third environments make use of a patchy distribution, which has a higher level of competition. In these environments a change in the levels of patch richness was found to produce significant differences in the levels of within-group cooperation, with a resultant P-Value of 0.003. This is because, with a higher level of competition, these environments have more room for patch richness to decrease the level of competition and in turn increase the environments carrying capacity.

While we failed to reject the null hypothesis in the case of uniformly distributed resource environments, we were able to reject it in the case of the more realistic patchy environments. We were therefore able to observe that the ABS simulation agrees with the second organizational trend mentioned by Reeve and Hölldobler and were able to accept *H2*, stating that "higher levels of patch richness lead to a higher degree of within-group cooperation".

From the Spearman rank correlations it was possible to discuss the four factors found by Reeve and Hölldobler which explain how changes in a system can bring rise to an increase in within-group cooperation. Where within-group cooperation is said to increase as (i) the group size decreases (a negative correlation), (ii) the number of competing groups increase (a positive correlation), (iii) the within-group diversity decreases (negative correlation) and finally (iv) the between-group diversity increases (positive correlation).

It was found that the results from all environments agreed with the first three factors mentioned. There was a slight difference found for the fourth factor. The expected result was a strong negative correlation, however, the second environment disagreed with this and held a neutral correlation instead.

Reeve and Hölldobler also mentioned that once a society moves towards the extreme of the superorganism continuum, due to ecological and genetic factors, the society has hit a theoretical "point of no return" in eusocial evolution.

Their reason for this point is the evolution of different castes of a species that have to work together in order to survive. This type of evolution is common amongst many eusocial insects [60, 49, 24, 11, 40]. While our simulation lacks the ability to simulate different reproductive castes of organisms, a similar "point of no return" is found in each environment. After the agents evolve to a specific level of within-group cooperation it is unlikely that a single mutation will result in the reintroduction of uncooperative individuals. Therefore our system represents a point where

Table 5: Statistical Results of Experiment 3, Testing the Impact of Higher Between-group Competition on Within-group Cooperation

Environment 3 Results, Correlations and Stable Ranges						
Relatedness Threshold	Within-group Cooperation	Between-group Cooperation	No Groups Formed	No Agents Per Group	Group Diversity	Population Diversity
0	0.037	1	1	7548.710	0.643	0.643
0.167	0.059	0.562	2.526	4819.840	0.556	0.596
0.333	0.053	0.595	2.372	5132.810	0.556	0.593
0.5	0.077	0.231	6.131	1732.810	0.449	0.549
0.667	0.843	0.131	22.972	12.157	0.063	0.554
0.833	0.863	0.134	22.909	5.008	0.061	0.563
1	0.941	0.119	30.674	3.466	0.012	0.565
Mean	0.410	0.396	12.655	2750.686	0.334	0.580
SD	0.443	0.335	12.403	3071.333	0.277	0.033
Correlation 1	-1					
Correlation 2	0.964					
Correlation 3	-0.964					
Correlation 4	-0.607					
Stable Range 1	From 0.167 to 0.333 no significant difference was found with a P-Value = 0.497 and $\alpha = 0.010$					
Stable Range 2	From 0.333 to 0.5 no significant difference was found with a P-Value = 0.03 and $\alpha = 0.013$					
Stable Range 3	From 0.667 to 0.833 no significant difference was found with a P-Value = 0.965 and $\alpha = 0.025$					

Table 6: Experimental Results Based on Patch Richness

Experimental Results Based on Patch Richness				
	Environment 1	Environment 2	Environment 3	Environment 4
Number of patches	1	1	5	5
Patch Richness	Base	Base + 50%	Base	Base + 50%
Within-Group Cooperation	0.111	0.116	0.077	0.097
Number Of Groups Formed	7.865	9.732	6.131	8.009
Number Of Agents Per Group	886.969	1547.864	1732.811	3605.664

agents act as a superorganism and require cooperation of the group to survive.

This research has contributed to the understanding of the origins of cooperation by commenting on various factors leading to its increase. From the results it was found that both relatedness and patch richness are precursors to within-group cooperation, with the level of competition emerging as an interesting factor possibly playing a large on the levels of cooperation found.

7. CONCLUSIONS

This study supports the effectiveness of agent-based models as complementary tools to mathematical models formulated about biological processes and using this information we were able to develop an ABS. This simulation allowed us to replicate the evolutionary and adaptive processes of nature, while observing the impact of changing key parameters (such as genetic relatedness and patch richness), which cannot be done in real-world biological experiments.

The results from this simulation agree with the first organizational trend presented by Reeve and Hölldobler and the first hypothesis of this study. Therefore genetic relatedness has a strong effect on the degree of cooperation experienced

contrary to the belief of studies by Nowak *et al.* [39] and Wilson [59]. In a similar vein to the results obtained by Reeve and Hölldobler, this simulation did not prove that relatedness is the only necessity for the occurrence within-group cooperation. Other factors, such as Patch Richness and environmental competition, were also found to play an effect.

A possible avenue of future work would firstly include a repetition of this study on more environments in order to compare the strength that both relatedness and patch richness have on the cooperation values obtained. Another addition may include different configurations of starting agents (number of agents, number of groups and so on), to determine if the evolution of the system was solely a consequence of the experimental measures or rather as a direct consequence of the configuration of starting agents in the environment.

8. ACKNOWLEDGMENTS

In the present case, the authors would like to thank Jacob Clarkson and Paul Wanjohi for their aid in the development of the experiment framework, and Geoff Nitschke for his guidance during the process of this study.

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