Effect of Colony Size on Inter-group Cooperation

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Cooperation in eusocial insect societies, such as ants, have been an intriguing social phenomenon. This guided researchers to investigate mathematical models that can explain this phenomenon. Examples of such models include: the kin selection theory, reciprocal altruism and tug-of- war theory. These models make certain abstractions that can be considered when designing agent-based systems. In this literature review, neuro-evolution will be shown to be an effective approach in designing and developing an agent-based system to simulate cooperation in an ant colony. Ultimately, this literature review will form the bases for the investigation of how colony size affects inter-group cooperation.

General Terms: Cooperation, Agent-based systems, Neuro-evolution

Additional Key Words and Phrases: kin selection theory, reciprocal altruism, tug-of-war theory, agent-based models

1. INTRODUCTION

Insect societies have long since fascinated researchers. In the past, evolutionary biologists have investigated the forces that have lead to the emergence of certain behaviours among social insects. In particular, entomologists and evolutionary biologists have been intrigued by the way cooperation evolves in a eusocial insect society. Various theories have been used to to explain how cooperation evolves in such societies with key mention: the kin selection theory (Hamilton, 1964), the reciprocal altruism mechanism (Trivers, 1971) and the tug-of-war theory (Reeve et al., 1998). The theories mentioned provide mathematical models that are used to understand how cooperation is achieved.

However, such mathematical models, such as Reeve and Hölldobler (2007) cannot account for the complexity in individual behaviours, and make lots of abstractions and simplifications. In this case agent based systems can simulate the conditions that give rise to cooperation and hopefully help support or refute existing biological hypotheses.

This literature review will cover cooperation in eusociality with key focus on how cooperation is typically modelled by biologists. Moreover, the review will investigate the use of agent based systems to model social behaviour in biological systems. Finally, the review will discuss methods that can be used to adapt individual (agent) behaviour in these agent-based systems, in particular, neuro-evolution as the candidate method.

2. COOPERATION IN SOCIAL INSECTS

The fascination of social insect societies has been owed to the altruistic nature of the individuals that form it. It is from this nature that cooperation emerges. Cooperation can be seen in social insects as they forage for food, defend and build the nest, and care for the brood. (Costa and Fitzgerald, 1996; Wilson, 1971) The interactions or social behaviour exhibited by an individual in a society influences the reproductive success of the society. In order to understand the genetic evolution of a behaviour, such as cooperation, evolutionary game theory and population genetics are identified as key approaches by Nowak (2012). Doebeli and Hauert (2005) supports this claim by highlighting the key concept behind cooperation as frequency-dependent selection - a concept well embodied in evolutionary game theory.

Models on the genetic evolution of cooperation have been considered as pairwise interactions between the cooperator and defector. Nowak (2012) introduces the term "cooperative dilemma", coined due to its similarity to the classic Prisoner's dilemma by Rapoport (1965), as a game between two strategies: cooperation and defection. Suppose that when a cooperator meets another cooperator they obtain a reward π, but if a

cooperator meets a defector then the cooperator gets siphoning pay-off σ, since the defector exploits the cooperator. When a defector meets a cooperator, he receives a tempting pay-off τ, but when faced against another defector a punishment ρ is given. (Hauert et al., 2006)

For a cooperative dilemma to occur, the rewarding pay-off of a cooperator- cooperator pair should be higher than than the punitive pay-off of the defector-defector pair, $\pi > \rho$. Secondly, there should be incentive for the cooperator to switch sides. The incentive can occur in one of three ways: (i) the tempting pay-off, when a defector meets a cooperator, is higher than the rewarding pay-off, $\tau > \pi$, (ii) the siphoning pay-off obtained by a cooperator would be lower than the punitive pay-off, $\rho > \sigma$ (iii) the tempting pay-off obtained by a defector would be higher than the siphoning pay-off the cooperator obtains, $\tau > \sigma$. (Nowak, 2012)

Rapoport (1965) defined the pay-off ranking for the Prisoner's dilemma as $\tau > \pi > \rho > \sigma$. Which implies that all three conditions for an incentive to occur, hold. This classifies the Prisoner's dilemma as the most rigid cooperative dilemma.

Among eusocial insects, the notion of defectors in the colony or society can be perceived as individuals that remain inactive while. Entomologists have observed puzzling trends among social insect colonies, where inactivity appears to be highly common to social insect colonies typically occupying more than 50% of the colony task time. (Charbonneau et al., 2015) Pinter-Wollman et al. (2012) highlights that individual workers do not simply differ in activity levels and argue that if that were so then individual activity levels could be predictable. However, they found consistent trends in activity levels across *related* tasks and worker cluster were formed that perform tasks in different situations frequently. By the mere existence of of cooperators and defectors in the society, it is fair to deduce that eusocial insect societies suffer from the cooperative dilemma.

Cooperation manifests itself amidst the cooperative dilemma especially if there are more cooperators than there are defectors. In the case, where the defectors are more than the cooperators, evolutionary tools must be used to evolve the social system to exhibit cooperation. The more rigid the social dilemma is, the more essential an evolutionary mechanism is to evolve cooperation in that society.

The importance of these evolutionary mechanisms is that without them, evolving societies facing the cooperative dilemma would evolve into a society containing only defectors. This is especially true if more than one of the conditions of the incentives for the cooperators to switch sides hold. Evolutionary mechanisms are helpful in propagating the cooperator genes in the society. In this section, this literature review will mainly discuss the evolutionary mechanisms that are used in evolving an eusocial insect society to exhibit cooperation.

2.1. Kin Selection Theory

Kin selection theory seeks to explain conditions in which altruism arises in an evolving society. The idea that altruism would arise in an evolving society would seem paradoxical. Altruism creates a situation in which an individual subordinates their own interest and those of their immediate offspring in order to serve the interest of a larger group. (Wilson, 1975) This would be in contrast to Darwin's theory of evolution by natural selection, as the genes promoting altruism are at a disadvantage in competition with genes that oppose it. (Darwin, 1859)

Cooperation among relatives can be explained by kin selection where selfish genes lead to unselfish phenotypes. (Hamilton, 1963) In kin selection theory, an individual assisting a relative indirectly promotes the transmission of copies of its genes to the next generation by a probability factor of their genetic relatedness. Hamilton's rule relates the change in actor's (cooperator) personal fitness c - also known as the cost

-, and the change in the recipient's personal fitness b - also known as the benefit - by a constant r that is the degree of genetic relatedness of the actor and the recipient. The rule states that for altruism to occur, equation 1 should hold for the altruistic individuals in the society. (Hamilton, 1963)

$$rb - c > 0 \tag{1}$$

In a paper identifying the flaws of Hamilton's argument, Wilson (2005) argues that the equation 1 defined as the Hamilton's rule does not cater for the case where the recipient and actor are not related, that is when $r = 0$. Among social insect societies, an altruistic individual would serve an individual that is not related to them. Consider a case where the recipient individual uses the cooperation strategy, it would then follow from the cooperative dilemma that the benefit b and the cost c are both greater than zero while the degree of relatedness $r = 0$. In such a scenario, the equation 1 would not hold.

Wilson (2005) proposes an correction to Hamilton's rule by suggesting that the benefit from collateral kin selection, b_k, be distinct from the benefit of accruing from colony-level selection independent of kin selection, b_e.

$$rb_k + b_e > c \tag{2}$$

Wilson (2005) highlights that in order for altruism to occur, the equation 2 holds for the altruistic individuals of the society. Furthermore, he claims that in nature the term b_e is overwhelming larger than rb_k, which implies that the colony level selection drives altruism in insect societies. This reduces equation 2 to $b_e > c$. Foster et al. (2006) refutes the claim by Wilson (2005) and mentions that true altruism can be achieved without kin selection. The result of this is a further alteration to equation 2 to a more explicit equation:

$$\frac{\beta}{n}(n - 1)r + \frac{\beta}{n}1 > c \tag{3}$$

where β is the group benefit (change in the group's fitness), n is the size of the group, c is the cost of the altruistic individual (actor) and r is the genetic relatedness of the actor and the recipient.

Foster et al. (2006) define $\frac{\beta}{n}(n - 1)$ as the kin benefit and the $\frac{\beta}{n}$ as the individual benefit (a share of the group benefit). Furthermore, they clarify that for true altruism the cost is greater than the individual benefit reasoning that altruism is individually costly. It thus follows that altruism in worker insects can only be selected if the relatedness is positive. (Wilson, 1990)

The essential characteristic pointed out by Keller and Chapuisat (1999) in eusocial insects is the reproductive altruism of the workers. While many worker insect remain sterile, they can transmit copies of their own genes by favouring the reproduction of their kin, such as siblings or cousins. It is this principle, introduced by Hamilton (1963) and further polished by Wilson (1990); Foster et al. (2006) that describe kin selection as an evolutionary mechanism for cooperation to flourish in an evolving society.

2.2. Reciprocal Altruism

In the previous subsection 2.1 this literature review has focussed on the interaction an altruistic individual has with the relative with little focus placed on the interaction between the altruistic individual and a non- relative individual. It is this consideration that led Trivers (1971) investigate reciprocal altruism as an evolutionary mechanisms that leads to cooperation in an evolving society.

Trivers introduces reciprocal altruism by focussing on the idea of the repeated Prisoner's dilemma, a stringent cooperative dilemma. (Nowak, 2006) Suppose that two

individuals play a game with the choice of two strategies: cooperation or defection. Further, suppose that these individuals are repeatedly faced against each other. The scenario posed where the individuals are exposed to symmetrical reciprocal situations is considered by game theorists as the repeated Prisoner's dilemma. (Luce and Raiffa, 1957; Rapoport, 1965; Nowak, 2006; Rubinstein, 1986)

Nowak (2006) documents some existing winning strategies to employing in the repeated Prisoner's dilemma. Among them are: *tit-for-tat* where an individual starts with cooperation and mimics the opponent's option onwards (Axelrod and Hamilton, 1981; Axelrod, 1984), *generous tit- for-tat* an individual opts for cooperation most times even when the opponent defects (Nowak and Sigmund, 1992) *win-stay* and *lose-shift* where an individual repeats their previous move if it was successful (Nowak et al., 1993).

Hamilton (1972) comments that for reciprocal altruism to occur, the individuals interacting together must remain together long enough for their roles as donor and recipient to be reversed several times. Furthermore, Nowak (2006) claims that reciprocal altruism can lead to the evolution of cooperation if the probability, w, of another encounter between the same individuals exceeds the cost-benefit ratio of the altruistic act:

$$w > \frac{c}{b} \tag{4}$$

The similarity equation 4 has to the origin Hamilton's rule (equation 1) is uncanny and can lead one to label w as the degree of "companion" relatedness of the individuals.

Trivers (1971) notes that reciprocal altruism has been well documented among human cooperation. Recently, experiments have been conducted in non-human societies supporting the rare influence of reciprocal altruism as mechanisms to achieve cooperation. (Hauser et al., 2009)

2.3. Tug-of-war theory

In the previous subsections 2.1 and 2.2, the theories presented outlined models that constrained the problem in a way that does not consider ecological, genetic and social factors experienced by the society. These factors should be considered when selecting a model.

Reproductive skew theories are theories that focus on the degree of reproductive bias in favour of dominant breeders. In high-skew societies, direct reproduction is performed by one or more dominant breeders in a group, while in low-skew societies, reproduction is distributed among the members. (Reeve and Keller, 2001)

Reproductive skew theories are divided into two models: transactional models and tug-of-war models. The focus of this literature review are the tug-of-war models. In this model, both the dominant and subordinate possess the power to influence the division of reproduction but this power comes at a cost. The cost incurred is a trade-off between maximising both the overall group productivity and the individuals' own share of the direct reproduction. (Johnstone, 2000; Reeve et al., 1998) Unlike the transactional model, the dominants and subordinates have limited control over the allocation of reproduction. (Reeve and Keller, 2001)

The model predicts that reproductive skew is negatively correlated to or independent of genetic relatedness between the dominant and subordinate. Langer et al. (2004) attributes this to the struggle over reproduction, an affair that takes place at the cost of overall group productivity. (Reeve et al., 1998)

In a paper exploring the theoretical consequences of a two tiered tug-of-war, Reeve and Hölldobler (2007) construct a model based off of the tug-of-war theory and predicts that within-group cooperation will decline as the between-group relatedness increases. Further, they highlight if between-group competition is much greater than within-group competition then the within group cooperation changes regardless of re-

latedness. Similarities can be drawn from the Reeve and Hölldobler (2007) model and the tug-of-war model.

3. AGENT BASED SYSTEMS

In the previous section, evolutionary game theoretic models are used to model cooperation in an evolving society of eusocial insects. However, due to the theoretic approach of the mathematical models presented, the complexity of the individual behaviour is not well accounted for by these models. The need for a model or system that accommodates this complexity while defining rules for the individuals to adhere to in a society arises.

Axelrod (1997) created among the first models with his evolutionary simulations of cooperative behaviour (first published in Axelrod and Hamilton (1981)) that was based on agent-based models. (Bryson et al., 2007) In agent-based models, each agent can perceive information and make decisions independently but constrained on some decision rules. (Zhong et al., 2014) They are often used to understand an observed behaviour, cooperation, in a social system can be considered by the the system's agents (individuals). (Bryson et al., 2007)

Agent-based modelling is a method for testing the collective effects of selections of actions an individual makes. A simulation based on these autonomous agents are ideally suited to explore the implication of non-linearity in system behaviour and also adapts to models that are easily scalable to scope and level. (Goldspink, 2000) Examples of such models are the game theoretic models described in section 2.

One of the differences that arises from agent-based systems and systems that are based off of simple agents (Epstein and Axtell, 1996), is the theoretical computation complexity of the two system. When dealing the latter kind of systems, application of the mathematical models is common for all agents; while in agent-based systems, emphasis is placed on the autonomy of each agent, which may require more computational resources. This difference is important especially when focussing on social systems with a very large number of individuals.

Furthermore, it is important to note that agent-based models require models or a set of rules that need to be tested. If the validity of the models in use is in question, so would be the agent-based model and by extension the agent- based system. Due to this nature in agent-based models, Goldspink (2000) classifies agent-based models as a social simulation meta-model and discusses its importance among organic social system.

4. NEURO-EVOLUTION

In this section, this literature review will focus on how the use of neuro- evolution can be used as an approach to construct agent-based systems.

Neuro-evolution is the application of evolutionary algorithms to the design and learning of artificial neural networks. (Yao, 1999; Floreano et al., 2008; Heidrich-Meisner and Igel, 2009) Neuro-evolution falls under the evolutionary algorithms which in turn is falls under the renowned sub-field of machine learning in the field of artificial intelligence. From this classification of neuro-evolution, it's definition can be further polished to include: neuro-evolution as a heuristic mechanisms used to prove theories through inference rules (machine learning nature) (Desai and Miikkulainen, 2000) and neuro-evolution as a means of evolving artificial neural networks. (Yao, 1999)

The effectiveness of the neuro-evolution algorithms lies in the effectiveness its constituent components: artificial neural networks (ANNs) and evolution algorithms (EAs). In the succeeding subsection, this literature review will delve into the components of neuro-evolution (EAs and ANNs). Ultimately, this review will analyse its use-

fulness as an algorithm for implementing agent-based systems introduced in section 3 over other machine learning approaches.

4.1. Artifical Neural Networks

Artificial neural network (ANN) modelling is a "black-box" non-linear machine learning technique which links input data and output data using a set of non- linear basis function. (Malinov et al., 2001; Heidrich-Meisner and Igel, 2009) ANNs in their own right consist of simple synchronous processing element, known as neurons, interconnected by synapses; an technique inspired by the biological nervous system. (Lippmann, 1987) There is a weight factor associated to each synapses.

Artificial neural network have largely been used in a number of classification tasks where the network seeks to match a set of inputs to a target output; as a result, they are able to develop predictive models for classification. (Russell et al., 1995; Malinov et al., 2001; Dreiseitl and Ohno-Machado, 2002; Tu, 1996)

In the case of agent-based systems with neuro-evolution, each individual is modelled with an artificial neural network and is used to determine the individual decision in the simulated environment. Construction of the neural network's topology is determined by the designer of the system. The most common implementation of the ANNs in neuro-evolution involves a set of inputs that are obtained from the simulated environment while the set of output would be the decision of the agent. (Russell et al., 1995)

The non-linearity of the neural network would prove advantageous to the construction of the agent based system as it will assist in exploring the implication of non-linearity of the social behaviour. Furthermore, autonomy of the agents in the simulation would be well defined by associating an artificial neural network to an agent.

4.2. Evolutionary Algorithms

Evolutionary algorithms is characterised by a population of solution candidates in this case the autonomous agents defined by their artificial neural networks. The reproduction process enables the combination of existing solutions to generate new solutions. (Abraham and Jain, 2005)

The evolutionary algorithm is inspired by natural selection where the gene of the fittest individuals in the population are propagated forward into the next generation of individuals. After a number of generations (a number that is dependent on the complexity of the system being simulated), the population should be filled with fit individuals.

From algorithm 1 an outline of an evolutionary algorithm is illustrated. It is used to find a target solution s_{target} within a population. It is important to note that this is a

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ALGORITHM 1: Outline of the Evolutionary Algorithm.

Initialise the target solution, s_{target}
Initialise the population, $P = \{p_1, ..., p_N\}$;
repeat
    Place individuals in the simulation for some period, t;
    for *each individual $p_i \in P$* **do**
        Calculate the fitness of p_i
    end
    Perform reproduction within the set P
    Replace weak agents with the children of P
until $s_{target} \in P$;
(see Russell et al., 1995; Cazangi et al., 2005; Abraham and Jain, 2005)

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just a skeleton of the processes used by evolutionary algorithm. For neuro-evolution, some clarification is needed to understand how algorithm 1 will be altered to for use within neuro-evolution.

Firstly, the target solution s_{target} may be defined as an observable attribute exhibited by an individual in the system while the individuals, p_i are defined as an encoding of the ANNs that govern them. In this case, s_{target} is said to be a *phenotype attribute* and the individual p_i are said to be the genotype, as it encodes an observable characteristics of the individual. In neuro-evolution, the genotype is an encoding of the neural network which can be encoded as an the weight values of the synapses with the individual ANNs.

Secondly, the reproductive process of the individuals makes use genetic operations: crossover (sexual reproduction), mutation (probabilistically altering the genes of an individual) and reproduction (surviving to the next generation unaltered). Koza et al. (2005, p. 34) clarifies that these genetic operations are applied to selected individual(s) on a probabilistic nature based on their fitness. This selection process favours the fitter individuals over weaker ones. However, the the fittest (or weakest) individuals may not necessarily be selected (or passed over).

Evolutionary algorithms owe their success to their effectiveness in searching for constructive strategies in a huge space of possibilities. The problem for evolution, as noted by Wright et al. (1968, 452-454), can be conceptualized as a search for, ideally, the global maxima in a multidimensional field of gene combination where height corresponds to fitness. Banzhaf et al. (1999) identifies the importance of genetic operations in achieving genetic diversity in the population. Genetic diversity allows for the exploration or exploitation of the search space; an identifying feature for evolutionary algorithms. The search becomes difficult as the dimensions and the number of local optima increase. (Axelrod, 1997) In order to reduce these factors, designing of the ANNs (genotype of the agents) should aim to make the ANN as lightweight as possible (with few weight values).

5. CONCLUSION

This literature review has considered the use of neuro-evolution as a strategy for implementing agent-based systems for modelling social behaviour in eusocial insect societies. It has been shown that neuro-evolution can be used to model complex social agents as it explores the implication of non-linearity of social behaviour with ANNs. Furthermore, its effectiveness of finding constructive solutions in a large search space makes it ideal for testing (or observing) emergent (or emerging) social behaviour. Ultimately, this literature review has shown that mathematical models (Reeve and Hölldobler, 2007) designed by evolutionary biologists and game theorists can be tested in a realistic simulation.

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