Qualities of Colony Insect Division of Labour Models

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Abstract

Successes of insect colonies inspired investigation of their adaptive division of labour. In addition to observing their behaviour, models have been created with the primary goal of testing hypotheses on the forces driving their division of labour. Using and improving these models for computational problems requires understanding them. As such, they are explained together with the ideas behind them. Followed by a comparison, investigating what has and hasn't been included in a model. The primary findings were that current models are relatively simple. Although, in most cases probably not simple enough to guarantee a full understanding of their behaviour. Additionally, an attempt towards a system integrating a majority of the suspected forces behind colony insect division of labour has not been made. Despite such a system potentially being able to mimic the success of the insects. Further work is needed to determine the usefulness of this class of models, and how they compare to each other and state of the art techniques.

Keywords: division of labour, adaptation, colony insects, swarm intelligence, modelling

1 Introduction

The enormous success of colony insects is evident from their wide spread and continued presence for over more than a 100 million years. Part of this success is believed to be a result of their effective division of labour strategies. Which include the ability to adapt the division of labour in response to changes in the environment. Investigating the workings of these division of labour strategies, biologists have created models aiming to replicate this behaviour. Most of those models include a small number of characteristics involved in division of labour and test the extend to which those succeed in reproducing insect behaviour.

Having a general interest in applying natures achievements in computer science, natural computing and in particular swarm intelligence logically have an interest in the computational relevance of those models. Up till now, division of labour models have not seen much use in application. While this could be due to the models not being very effective, no proof seems to exist to support that. Nor does there seem to be much in terms of a showcase comparing the models, either to each other or to state of the art algorithms in possible application areas.

The focus of this paper is on making the state of the art in colony insect division of labour research accessible to computer scientists and hopefully non-biologists in general. This is necessary in order to create a basis for empirically testing these methods and hopefully showing their applicability to real world problems. As such, the primary goal is to explain the major models that were created, where they come form and fit in with regard to colony insect behaviour, and the extend to which they have been applied in computer science.

This work proceeds by describing the various characteristics involved in division of labour that can be observed in colony insects in Section 2. Following that, Section 3 describes models of division of labour that have been proposed. Section 4 then compares the models to see which characteristics are being used and where various models have found application so far. Finally, Section 5 contains the discussion and deals with what future developments and research may be interesting in this field, from the perspective

of a computer scientist.

2 Division of labour characteristics

Division of labour models are based on a number of characteristics observed in nature. This section aims to provide an overview of those characteristics and the frequency of their presence in the variation of colony insect species. These descriptions are primarily based on the review work by Beshers and Fewell (2001 [4]) and Duarte, Weissing, Pen and Keller (2011 [20]). Since these works are from 2001 and 2011 respectively, this should provide a reasonable view on the current state of division of labour research.

Temporal polyethism, or division of labour based on age, is believed to be present in many social insect species (Wilson 1971 [75], Oster and Wilson 1978 [44]). When observed in nature this is characterised by younger workers performing tasks within the nest, like brood care, while older workers take up tasks outside the nest, such as foraging and nest defence (this was reviewed by G.E. Robinson 1992 [53]). The transitions to different tasks during the ageing process have been associated with physiological alterations like changes in the concentration of the juvenile hormone (a hormone believed to regulate many aspects of physiology in insects) and the vitellogenin protein in honey bees (G.E. Robinson 1987 [52]). Moreover, E.J.H. Robinson, Feinerman and Franks (2012 [51]) suggested that the early discoveries of division of labour based on age may be covering up other regulators of division of labour. One example is corpulence (fat reserves), which proved a better predictor in their study of the *Temnothorax albipennis* ant. They further suggest that due to the frequent correlation between age and corpulence (Porter and Jorgensen 1981 [47], MacKay 1983 [40], Tschinkel 1998 [71], Toth and G.E. Robinson 2005 [69]), this may also have been overlooked in other species. In turn, the results of Franklin, E.J.H. Robinson, Marshall, Sendova-Franks and Franks (2012 [25]) suggest that experience is a better indicator for the likelihood of workers participating (and especially leading) in tandem runs (a one on one recruitment method) than age in the same ant species. Together, this promotes caution in attributing division of labour to temporal polyethism, but certainly does not invalidate it altogether. Note that the term temporal polyethism is, confusingly, at times being used to refer to both age differences causing division of labour and the distribution of different age groups over different tasks, as a result of other factors. This work will use it to refer to a relation between age and division of labour, regardless of cause.

Morphological polyethism, or size and shape related division of labour, is present in termites and those ant species with clearly distinguishable subcastes (Oster and Wilson 1978 [44]). In almost all of the studied species this was an indicator of worker behaviour (Wilson 1980 [76], Detrain and Pasteels 1991 [16], E.J.H. Robinson, Feinerman and Franks 2009 [50]). While the manifestation of morphological polyethism differs among species, it seems to hold that more extreme morphological differences result in more specialised behaviour of castes and smaller task repertoires (Oster and Wilson 1978 [44]). Morphological specialisations mostly focus on foraging and defence, some less common specialisations are food processing and storage (Hölldobler and Wilson 1990 [29]). An example can be found in the ant genus *Pheidole* (a genus believed to consist of about 1,000 species (Wilson 2003 [78])), where major and minor workers specialise on different sets of tasks (Wilson 1985 [77], Mertl and Traniello 2009 [42]). Although morphological castes specialise on a certain task repertoire, it seems that they do maintain some flexibility in task choice (Detrain and Pasteels 1991 [16]).

Genetic variation is present in species where the queen mates with multiple male drones, like in honey bees and leaf-cutter ants (G.E. Robinson and Page 1989 [55], Julian and Fewell 2004 [33], Fournier, Battaille, Timmermans and Aron 2008 [24], Waddington, Santorelli, Ryan and Hughes 2010 [73]), as well as in species with multiple queens (Snyder 1992 [62], Blatrix, Durand and Jaisson 2000 [6]). This respectively results in multiple patrilines and matrilines (groups with the same line of male or female ancestors). These patrilines and matrilines may lead to different preferences towards which tasks are performed, but this is not always the case (Fournier et al. 2008 [24]). In fact, there are indications that whether or not there is an influence on task preference is variable over time (years) and the environment (Falconer and Mackay 1996 [21], Larsson, Rattiste and Lilleleht 1997 [37], Rüppell, Heinze and Hölldobler 2001 [59]). There exists little evidence that genetic diversity

has a positive effect on the efficiency of the colony (Rosset, Keller and Chapuisat 2005 [58], Fournier et al. 2008 [24]). An alternative explanation for the existence of this genetic diversity may be an increase in a colony's resistance to parasites (Baer and Schmid-Hempel 1999 [3], Tarpy 2003 [64], Wilson-Rich, Spivak, Fefferman and Starks 2009 [79]).

The **Colony life cycle** of a social insect colony generally goes through three phases. First, a new nest is founded by a newly mated queen (and a king in termites). This is followed by a quick growth stage in which only workers are produced. Finally, there is a transition to the reproduction stage, mostly when a certain colony size is reached (varying between species), where new sexuals (males and gynes (reproductive females)) are produced (Oster and Wilson 1978 [44]). In the first phase, species with morphological castes only produce small workers. As the colony gets larger, the average worker size also increases (Hölldobler and Wilson 1990 [29]). Over the lifetime of a colony task needs like nest building and foraging change, while the need for other tasks, like maintaining the temperature and humidity condition, is relatively stable. An example of this can be observed in the *Lasius niger* ant, where the distribution of workers over tasks changes over the growth of the colony (Mailleux, Deneubourg and Detrain 2003 [41]). It has been suggested that colony size affects the complexity of social behaviour and division of labour, smaller colonies should have more generalist workers (Karsai and Wenzel 1998 [34], Bourke 1999 [10], Anderson, Franks and McShea 2001 [2]). The ant *Rhytidoponera metallica* supports this, since age based division of labour is clearly present in large colonies, but not in small ones (Thomas and Elgar 2003 [66]). The *Temnothorax albipennis* ant has a clear difference in the number of brood-carrying specialists during emigration, depending on colony size. Compared to small colonies, large colonies have a larger proportion of these specialists (Dornhaus, Holley, Pook, Worswick and Franks 2008 [18]). Generally speaking, there does however not seem to be a difference in the level of division of labour depending on colony size in this species (Dornhaus, Holley and Franks 2009 [17]).

Experience of individual ants affects task preference in the thelytokous (females produced from unfertilised eggs) ant *Cerapachys biroi*. Individuals with the same age had a clear distinction in task preference between those that had successful foraging experience and those that did not (Ravary, Lecoutey, Kaminski, Châline and Jaisson 2007 [49]). In the non-thelytokous *Temnothorax albipennis* ant, when the normal predictor for foraging (corpulence) is equal in two ants, the ant with a recent successful foraging trip is more likely to go foraging (E.J.H. Robinson et al. 2012 [51]). Moreover, when performing tandem runs (leading a single other ant to a target) experienced ants of the same species are more likely to lead and they perform the task more accurately. Meaning that they walk slower (to maintain follower contact) and have a more precise bearing on the target (Franklin et al. 2012 [25]). It would be interesting to investigate the extend to which the use of experience in task choice can be generalised, both in thelytokous and non-thelytokous species.

Environmental stimuli have an influence on the decision of whether or not to perform a task. For example, in the red harvester ant (*Pogonomyrmex barbatus*) the return rate of successful foragers is observed. This is likely to be a good indicator of the availability of food. When the return rate of successful foragers increases, the departure rate of inactive workers also increases, unsuccessful foragers have no impact (Schafer, Holmes and Gordon 2006 [60]). Adaptation to food availability is also found in the *Pheidole morrisi* ant. In this ant a sub-caste of majors can be identified, called repletes, which serve to store fat. During the autumn season, the number of repletes increases to prepare for winter. Moreover, across all workers the fat storage is also increased (Yang 2006 [80]). In the ant species *Pogonomyrmex desertorum*, activities outside the nest are temporarily stopped in response to predation (Munger 1984 [43]). The same was reported for the *Pogonomyrmex rugosus* ant. Which, possibly to make up for the temporary inactivity, when it later returns to foraging seems to be be more active than before (MacKay 1982 [39]).

Developmental factors are also believed to influence task choice in social insects. The *Camponotus rufipes* ant shows this in its response to temperature changes. The temperature experienced during larval development later influences at which temperatures brood is moved (Weidenmuller, Mayr, Kleineidam and Roces 2009 [74]). Brood movement is important due to the optimal developmental temperature and avoidance of potential brood mortality at extreme

temperatures. Other factors such as light and humidity may also affect task preference, though those are yet to be studied.

Social interaction between workers can also influence the task choice. An example can be found in the honey bee. When foragers return to the nest they transfer the nectar to food-storers, which, as is implied, then store the nectar in the nest. In this situation the forager has to find a food-storer, if this is a short search, more foragers will be recruited (Seeley and Tovey 1994 [61]). As mentioned earlier in relation to temporal polyethism, hormones play a role in the transition to becoming a forager in honey bees. Changes in the hormonal titres (a way to express concentration) have also been associated with interactions between workers, during which foraging-inhibiting substances are transferred (Huang and G.E. Robinson 1996 [31], Leoncini et al. 2004 [38]).

3 Division of labour models

Based on the behaviour of colony insects various division of labour models have been proposed. This section discusses a number of popular models. The workings of each model will be explained, followed by a description of how this was mathematically modelled. Here, like in the previous section, the reviews by Beshers and Fewell (2001 [4]) and Duarte et al. (2011 [20]) served as a basis for the descriptions. The evolutionary models of division of labour discussed by the later are not included here, because, while very interesting, they exceed the scope of this work.

The **response (or fixed) threshold model** is based on the idea that workers have an internal threshold for every possible task. How the thresholds are determined for individual workers varies among different versions of this model, but for the basic response threshold model these thresholds are fixed. By default a worker will do nothing (G.E. Robinson and Page 1989 [54], Page and Mitchell 1990 [45]), when it is somehow stimulated for a specific task it may be incited to perform it. Whether or not the worker performs that task depends on the strength of the stimuli. When this stimuli passes the internal threshold for this task, the worker will perform it, otherwise it will not. Among the various versions these stimuli tend to be global, meaning that they are the same for every worker in the colony. Whenever a task is performed the global stimulus level for

that task is decreased. Thanks to this, workers with a higher threshold for this specific task may never be incited to perform it. Together, this can result in workers with slightly different thresholds having vastly different task repertoires and differences in the frequency of task performance (Fewell and Page 1999 [23]).

Equation 1 shows how Bonabeau, Théraulaz and Deneubourgh (1996 [8], 1998 [9]) modelled response threshold behaviour. Here $T_{\theta ij}$ is the probability of individual i to perform task j, provided the strength of the stimulus s and a response threshold θ. In their model, the colony wide stimulus level was increased constantly by a parameter δ and decremented for every task performed.

$$T_{\theta ij}(s_j) = \frac{s_j^2}{s_j^2 + \theta_{ij}^2} \qquad (1)$$

The **self-reinforcement model** works by lowering the threshold of a task in response to performing it. Conversely, the threshold is increased for tasks that are not being performed by that worker. These alterations to the threshold result in workers being more likely to take on tasks they are experienced in.

Plowright & Plowright (1988 [46]) mathematically modelled self-reinforcement as in Equation 2. In the model, the probability of performing the task P was influenced by the external stimulus E and the internal reinforcement I, provided a constant K.

$$P = 1 - e^{-IKE} \qquad (2)$$

The **reinforced threshold model** has the same properties as the response threshold model. With the difference that thresholds are reinforced over time, as in the self-reinforcement model.

To model the reinforced threshold concept, the update rule in Equation 3 was introduced by Théraulaz, Bonabeau and Deneubourg (1998 [65]) for the response threshold model described in Equation 1. Once again, θ_{ij} is the response threshold for of individual i for task j. Then, ξ is the learning coefficient and φ the forgetting coefficient, for a time period Δt. Finally, x_{ij} is the fraction of time within Δt that an individual i performs task j and $1 - x_{ij}$ that it does not. As such, depending on how much time a worker is active for a specific task, it will learn or forget the task by respectively de- or increasing the threshold for that task.

$$\theta_{ij} \rightarrow \theta_{ij} - x_{ij}\xi\Delta t + (1 - x_{ij})\varphi\Delta t \qquad (3)$$

Foraging for work is a model that investigates how a worker's location impacts task choice (Tofts and Franks 1992 [68], Tofts 1993 [67]). In this model, tasks are ordered as in a production line, each following after another. Workers start at the first task and pass on the product of that task to the next, until it reaches the last. The algorithm works by having workers perform any available task. Once done, they will try to perform the same task again. If there is no more work to be done for this task, they will move to another task and attempt to work there.

Social inhibition assumes that workers have an intrinsic activator pushing them to start foraging. As they age, the activator becomes stronger and they eventually switch from in nest tasks to foraging. The rate at which workers become foragers is then regulated by inhibitors passed to nest workers by foragers. With a larger number of active foragers, the inhibition applied through social interaction is greater, due to which fewer nest workers switch to foraging. If there are too few foragers, inhibition will decrease and nest workers may switch task. Note that the idea of the activator was based on a correlation between the juvenile hormone and the behavioural development of workers (Huang and G.E. Robinson 1992 [30], 1999 [32]). It has since been shown that behavioural development does not require the juvenile hormone, although it is still involved (Sullivan, Jassim, Fahrbach and G.E. Robinson 2000 [63]).

A mathematical model for social inhibition was described by Beshers, Huang, Oono and G.E. Robinson (2001 [5]). In the model, the behavioural development is represented by x, which is the change in the physiological state from one day to the next. These changes are regulated by the average x of the colony through rules that map workers' their x at time t to x at $t + 1$.

The **network model**, defined by Gordon, Goodwin and Trainor (1992 [28]), allows workers to be in one of eight states. These states express four different tasks for which a worker can either be active or inactive, divided over two subclasses of two tasks each. In the model, all workers are internally the same, the distribution of tasks results from interactions between them. These interactions allow for an assessment of the worker distribution over the tasks and the distribution over the active and inactive state of a task. An active worker will exchange information with all other active workers and with the inactive workers of the task it is active in. Inactive workers only exchange information with workers assigned to the same task, regardless of whether they are active or not. Depending on information received through their interactions, workers may decide to change state based on a predetermined optimum distribution.

A set of three mathematical decision rules, dependent on the received information, were defined by the same authors. These rules result in decisions on (a) being active or inactive, (b) which subclass the worker is in and (c) which of the tasks in the subclass is chosen.

4 Model comparison

In order to make a comparison between the models discussed in the previous section, a number of things are taken into consideration. For each model the characteristics, as defined in Section 2, they incorporate are looked at. Incorporate here means: *what can be observed in the model*. Note that this leaves room for discussion about how strongly such a characteristic is associated to the model, since it may not have been taken into consideration when the model was constructed or have an explicit representation. Further, the areas in which the model has seen application in computer science are discussed, where such works have been found.

The **response threshold model** is based on the genetic and environmental stimuli characteristics. It can also be used to explain morphological polyethism, provided that morphologically different workers are initialised with a different threshold distribution. This model and its derivatives (as will become evident with the reinforced threshold model) are probably the most popular in application. For example, it was used in combination with particle swarm optimisation (Vesterstrøm, Riget and Krink 2002 [72]). Another application was in robotics (Krieger and Billeter 2000 [36], Agassounon and Martinoli 2002 [1]).

Self-reinforcement clearly incorporates experience by favouring tasks that have been performed before. In order to be able to incite task performance in the first place, external stimuli are involved. Since experience influences a threshold, this needs to be initialised just like in the response threshold model.

Models	Temporal polyethism	Morphological polyethism	Genetic variation	Colony life cycle	Experience	Environmental stimuli	Developmental	Social interaction
Response threshold		✓	✓			✓		
Self-reinforcement		✓	✓		✓	✓		
Reinforced threshold		✓	✓		✓	✓		
Foraging for work	✓				✓	✓		
Social inhibition	✓			✓				✓
Network								✓

Table 1: Which characteristics can be observed in which models?

As such, here too a relation can be seen to the genetic and morphological characteristics. This model doesn't seem to have been used in application.

Since the **reinforced threshold model** is a combination of the two previously mentioned models, it thus logically incorporates the union of their characteristics. This is however the same as the set of characteristics of the self-reinforcement model. Which poses the question of how different the self-reinforcement and the reinforced threshold model really are. It would seem that only their mathematical representation differs, while the ideas behind them are the same. An empirical comparison of the two may show whether they actually result in different behaviour or which is the most efficient implementation, if they prove to behave identically. This model saw application in a number of fields like scheduling (Campos, Bonabeau, Théraulaz and Deneubourg 2000 [11], Cicirello and Smith 2001 [12] [13], 2003 [14], Kittithreeerapronchai and Anderson 2003 [35], Cicirello and Smith 2004 [15]), mail retrieval (Bonabeau, Sobkowski, Theraulaz and Deneubourg 1997 [7], Price and Tiňo 2004 [48]) and multi agent systems (Ferreira, Oliveira and Bazzan 2005 [22]).

Foraging for work proves that labour does not need to be divided based on age for temporal polyethism to evolve. Relations to experience can also be observed. After all, in this model a worker is more likely to perform a task it has performed before, i.e. in which it has experience, since the model forces them to try to perform the same task again before moving to another. Additionally, there is a relation to the environmental stimuli characteristic in that stimuli will differ depending on where the worker is in the line of tasks. This model has had quiet a back and forth of critiques (G.E. Robinson, Page and Huang 1994 [56], Franks and Tofts 1994 [27], Robson and Beshers 1997 [57], Traniello and Rosengaus 1997 [70], Franks, Tofts and Sendova-Franks 1997 [26]). However, these were primarily biologically based. As such, while the model's biological validity has been questioned, it may well be viable in application, although it has not seen use yet.

In **social inhibition** temporal polyethism is clearly present in that the activator changes while a worker ages. Since the interaction between workers regulates the distribution over the tasks, social interaction is also definitely a part of this model. The colony life cycle can also be observed here, in that in newly founded colonies there may be fewer foragers to inhibit nest workers, leading to faster development into foragers and vice versa. Social inhibition has been used as inspiration for some division of labour mechanisms in swarm robotics (Zahadat, Crailsheim and Schmickl 2013 [81]).

The **network model** obviously incorporates social interaction, which allows workers to approximate the

task distribution. Through the presence of subclasses in tasks, the model may seem to incorporate the possibility for genetic or morphological task preference. This is however negated by the fact that the network model enforces that each worker is internally identical. No works on the application of this model were found.

As becomes evident when looking at Table 1, differences in task choice resulting from developmental variation are not represented in the considered models. This may be due to the smaller amount of research done in this area compared to the other characteristics. On the other hand, by not including it in the models nothing is learned in regards to its effect on division of labour either.

Another observation is that some major characteristics do not, or rarely, occur together in a model. For example, the interactions between temporal and morphological polyethism, or social interaction and experience, may result in interesting dynamics.

Except for the network model, all of the other considered models incorporate three or more characteristics. This is obviously not ideal to determine what exactly causes which effect in the behaviour of a model. Admittedly, this is in part due to how the association to characteristics were determined in this work. Yet, the majority do in fact have more than one characteristic at their basis. Measuring the effects of individual characteristics would be useful in analysing their exact behaviour.

5   Discussion

Adaptive task allocation works (is effective) in nature. Therefore, if a computational model can accurately represent nature, it should also provide adaptive task allocation. Such a model may not be the most efficient (in terms of computational resources and time), nor give the absolute optimal task allocation, while maintaining flexibility to respond to change. It can however serve as a baseline for performance. Creating a truly accurate model with the current biological understanding is not realistic. There does however not seem to be a model that even gets close to incorporating all aspects of the current understanding of colony insect division of labour. Such a model could serve both to further the biological understanding of division of labour and to set a computational baseline with a, reasonably close, representation of a proven system.

In response to critiques of their foraging for work model Franks et al. (1997 [26]) argued that a good model is simple. While a legitimate argument, there is value in both very basic models and more elaborate ones. Such more elaborate models will be able to show the effects of the interactions between their individual parts. A lot remains to be learned in the process of experimenting with continually larger groups of characteristics, slowly leading to a complete model. Of course, care needs to be taken that during this process no unnecessary complexity is introduced into such a model. Obviously, models consisting of smaller sets of characteristics produced during this process could be more effective or efficient for certain applications, depending on requirements of the problem they are applied to.

The understanding of the, relatively, simple models discussed in Section 3, would greatly improve if they were showcased in an application area, aside from the popular (reinforced) response threshold models this is currently missing. Comparing all these models on a set of problems can make for a good view on their strengths and weaknesses. Those problems can be either benchmarks or real world applications. Both should result in interesting insights into the behaviour of these models. Note that, while for this work no application was found for the majority of models, the search was hardly exhaustive and there may in fact be some uses out there.

In addition to studying the workings of those models, comparing them to state of the art approaches will also be valuable. This can be done with state of the art techniques used in application areas mentioned in Section 4, as well as other potential application areas.

Duarte, Pen, Keller and Weissing (2012 [19]) took an approach combining division of labour with evolution. Despite being beyond the scope of the comparison made in the previous section, this is an interesting advance in the field requiring additional work. While they question whether their use of the threshold model in their experiment is the ideal approach for combining the two, their results do show that division of labour can emerge through evolution. Incorporating this evolutionary concept into division of labour models may have added value through allowing the model to adapt its distribution mechanisms over time. Once a thoroughly tested evolutionary approach exists, it should be possible to create mod-

els that adapt to changes in the number of tasks, specialised castes, matings and more. Obviously, the idea of a model that is able to provide (reasonable) optimisation to a problem that changes over time is an ambitious one with many challenges, but if this is achieved, it could serve as a solution in many areas.

In short, future work should focus on both further individual investigation of models and their characteristics to improve the understanding of their behaviour, as well as integrating them to study the effects they have on each other. Comparisons between each of the models and state of the art techniques will then identify their individual use cases or lack thereof.

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