The Evolution of Temporal Polyethism

Heather J. Goldsby[1], Neem Serra[1], Fred Dyer[2], Benjamin Kerr[1], Charles Ofria[2]

[1]University of Washington, Seattle, WA 98195
[2]Michigan State University, East Lansing, MI 48824

Abstract

Temporal polyethism is a method of division of labor exhibited by many eusocial insect colonies, where the type of task an individual attempts is correlated with its age. The evolutionary pressures that give rise to this widely-observed pattern are still not fully known. The long generation times of eusocial insects combined with the complications associated with performing artificial selection experiments on colonies of organisms makes this topic challenging to investigate using organic systems. In this paper, we use digital evolution to explore whether temporal polyethism may result from pressures to preserve colony members in the face of varying degrees of risk associated with different tasks. Specifically, we require a colony of digital organisms to repeatedly perform a set of tasks in order for the colony to replicate. We associate the different tasks with different lethality risks. Under these conditions, we observe that the digital organisms evolve to perform the less risky tasks earlier in their life and more risky tasks later in life, regardless of the order in which the tasks were performed by the ancestor organism at the start of the experiment. These results demonstrate that pressures resulting from the relative riskiness of various tasks and aging is sufficient to favor the evolution of temporal polyethism.

Introduction

Division of labor, where individuals specialize on specific roles and cooperate to survive, is hailed as a strategy central to the success of eusocial insect, crustacean, and mammal colonies (Crespi, 2001; Duffy, 2003; Hölldobler and Wilson, 2009; Jandt and Dornhaus, 2009; Queller and Strassmann, 2003; Wilson, 1980). Within nature, eusocial organisms are renowned for exhibiting *reproductive division of labor*, where members of the reproductive caste (i.e., queens) produce offspring and members of the non-reproductive caste care for the brood and perform other duties central to the maintenance of the eusocial colony (Jandt and Dornhaus, 2009). Moreover, many eusocial organisms, such as leaf-cutter ants (Wilson, 1980), bumblebees (Jandt and Dornhaus, 2009), and aphids (Pike and Foster, 2008), also exhibit *task-related division of labor*, where individuals specialize on performing a particular task. For example, non-reproductive worker bumblebees specialize to perform roles that include foraging, caring for the brood, building honeypots, guarding the hive, or cooling the hive through fanning (Jandt and Dornhaus, 2009).

One form of task-related division of labor exhibited by many eusocial colonies is *temporal polyethism*, where a worker's age is correlated with the type of task it performs (Franks et al., 1997; Hölldobler and Wilson, 2009; Robson and Beshers, 1997; Sendova-Franks and Franks, 1993; Tofilski, 2002; Tofts, 1993; Traniello and Rosengaus, 1997). For example, within a honeybee colony, a worker bee may progress sequentially through four castes: cell cleaning caste, broodnest caste, food storage caste, and forager caste (Seeley, 1982). Within ant colonies, a similar shift is performed from activities within the nest, such as brood care, to foraging activities outside the nest (Hölldobler and Wilson, 2009). Researchers are still actively exploring the causes and mechanisms underlying this division of labor pattern. In this paper, we study the evolutionary conditions that can give rise to temporal polyethism.

Two hypotheses have been proposed to explain temporal polyethism. The *task-riskiness* hypothesis posits that an individual's age is causally linked to the task that it performs (Hölldobler and Wilson, 2009; Robson and Beshers, 1997; Traniello and Rosengaus, 1997). This causal relationship is thought to have evolved because of a pressure to conserve work force members and thus to have older members (who are closer to death) perform more risky tasks (Hölldobler and Wilson, 2009). For example, foraging, a task commonly responsible for the loss of 1% to 10% of the colony population per day (Hölldobler and Wilson, 2009), is performed when the organism is likely to die of natural age-related causes and thus is more expendable. In this way, the colony optimizes the use of its workers. (Tofilski, 2002). In contrast, the *foraging for work* hypothesis assumes that as organisms are born they perform tasks closest to them and proceed to perform tasks further from the center of the nest (Franks et al., 1997; Hölldobler and Wilson, 2009; Sendova-Franks and Franks, 1993; Tofts, 1993). This explanation depends only upon organisms' reactive responses to task stimuli. Thus, according to the foraging

for work hypothesis, colonies exhibit a temporal polyethism pattern as a result of the spatial organization of the colony's nest without any inherent evolutionary advantage related to the riskiness of any task.

Studies have produced evidence in support of both hypotheses (Franks et al., 1997; Hölldobler and Wilson, 2009; Robson and Beshers, 1997; Traniello and Rosengaus, 1997). Specifically, studies with monomorphic ants provide support for the foraging for work hypothesis by presenting evidence that the task riskiness hypothesis is too rigid to account for the unstable situation of ants and any correlation of age and task is merely a byproduct (Sendova-Franks and Franks, 1993). In the original foraging for work mathematical model created by Tofts, ants change tasks when work was unavailable at the current location (Tofts, 1993). In one study, marking the ants showed that older ants were flexible in the tasks they performed, and all ants, regardless of age, foraged for work, meaning that they actively sought out tasks to perform (Sendova-Franks and Franks, 1993). However, critiques of Tofts' model of foraging for work highlight that the way in which workers can move between tasks creates a biologically unrealistic colony (Robson and Beshers, 1997). Others have noted that Tofts' model does not account for many other eusocial insects, such as termites, that have a well-developed age-based division of labor strategy that is not a byproduct of foraging for work (Traniello and Rosengaus, 1997). In addition, an alternative mathematical model testing the task-riskiness hypothesis was created with a set of two tasks that each had a different mortality rate (Tofilski, 2002). This model shows that the longevity of workers in a colony that perform tasks without regard to the amount of risk associated with them is significantly lower than the longevity of workers a colony that perform tasks in order of risk (Tofilski, 2002).

While these studies have examined potential proximate causes of temporal polyethism exhibited by current eusocial colonies, it is challenging to explore the evolutionary conditions that may give rise to this pattern. Both field observations and experimental studies of evolution in lineages of actual organisms are infeasible because of long generation times and the complexity of studying large social groups in a controlled way.

To address these challenges, we use Avida, a digital evolution software platform that maintains a population of self-replicating computer programs in a user-defined environment (Ofria and Wilke, 2004). Each computer program is a digital organism that executes its genome (a list of computer instructions) to perform tasks, where the tasks enable the organism to collect resources and thus compete with its neighbors. Avida meets all of the requirements for evolution: replication, variation, and differential selection. Avida has previously been used to study topics such as division of labor (Goldsby et al., 2012), origin of complex features (Lenski et al., 2003), and evolution of cooperation (Knoester et al.,

2007). Digital organisms have rapid generation times (e.g., thousands of generations in a few hours), thus enabling us to study this complex evolutionary phenomenon.

In this paper, we use Avida to explore whether varying the amount of risk associated with tasks is sufficient to evolve colonies that exhibit a temporal polyethism structure. We created a world in which different tasks were associated with different levels of risk. We used colonies of clonal (i.e., genetically identical) organisms, where the colonies competed for limited space in the Avida world. Each colony was required to perform each type of task a certain number of times for the colony to replicate. An ancestor organism performed each of the required tasks once. We explicitly removed any spatial component to task performance to determine whether organisms were responding to the spatial structure of the nest, or the risk associated with tasks. In response to these pressures, the organisms evolved division of labor strategies in which tasks associated with less risk were done earlier in an organisms life and riskier tasks were performed later in life, regardless of the initial order of the tasks. These data provide support for the hypothesis that risks associated with aging and various tasks are sufficient to produce temporal polyethism.

Methods

To use Avida to study the evolution of temporal polyethism, we created a world consisting of competing colonies that each contain a set of clonal organisms. Each of digital organisms has a virtual CPU, a genome (a circular list of computer instructions), and a location within the colony. The virtual CPU of an organism consists of three general-purpose registers and two stacks. Each digital organism executes instructions on its virtual CPU. The instruction set in Avida allows for basic computational tasks, such as addition, multiplication, and bit-shifts, controlling the execution flow, and self-replication. An organism performs logic operations (NOT, NAND, etc.) called *tasks* by executing the instructions in their genome.

For a colony to replicate, the organisms within that colony must perform each type of task in a set a certain number of times. For example, in our initial experiments, a colony had to perform task NOT 250 times and task NAND 250 times. A natural analog is a colony of eusocial insects in which the workers must both forage for food and tend to the brood. In addition, because each colony starts with only one organism, organisms must also replicate to produce other organisms that can assist them in the performance of tasks to achieve the overall colony objective. During colony replication, the genome of the colony is potentially mutated (i.e., instructions are potentially inserted, removed, or exchanged for other instructions). This new genome is used to seed a daughter colony, which is selected randomly from the colony population.

To address our central question regarding the evolution of

temporal polyethism, we added the capability for each task to be associated with a *lethality risk* that specifies the probability of the organism dying before completing the task. Non-risky (or safe) tasks have a lethality risk of 0. Our most risky tasks have a lethality risk of 25%. If an organism is killed while performing a task, then the task is not completed and thus does not count toward the task count of the colony.

In most other Avida experiments, organisms are reset upon producing an offspring, in order to emulate the behavior of bacteria that divide into two daughter cells when they replicate. However, since age and internal state play a key role in these experiments, we modified the organisms so that they do not reset after replication, but rather just continue running.

At the outset of these experiments, we seed the colonies with an *ancestor* organism that performs all the types of tasks necessary for completion of the colony task. In our experiment, an ancestor organism performs task NOT and task NAND once. Because each colony contains only one individual at the onset of the experiment and also after colony replication, organisms must self replicate to fill the colony. Each experiment comprises several different treatments that randomize the order in which the tasks appear in the ancestor organisms' genomes, as well as the riskiness associated with the tasks.

The starting world for each experiment had 400 colonies each of which contained one ancestor organism. Organisms were subject to three mutation rates during colony reproduction: a copy mutation rate of 0.0075 (0.0003 per instruction), an insertion mutation rate of 0.05 (0.002 per replication), and a deletion mutation rate of 0.05 (0.002 per replication). For each experiment, we conducted 30 trials to account for the stochastic nature of evolution. Each trial ran for 100,000 updates, where an *update* is the amount of time it take an average organism to execute 30 *cycles* – each instruction takes one cycle to execute.

Results

The primary topic of this study is whether the risks associated with aging and tasks are sufficient to evolve colonies of organisms that exhibit temporal polyethism. For our study, we created a two-task environment in which colonies had to perform task NOT 250 times and task NAND 250 times in order for the colony to replicate. We created four risk treatments (described in Table 1) that vary the lethality risks associated with the tasks. Specifically, the treatments are: (1) task NOT is risky, (2) task NAND is risky, (3) neither task is risky (a control), and (4) both task NOT and task NAND are risky (a control).

Additionally, we created two possible ancestor organisms (depicted in Figure 1). Each ancestor completes each task once and then self-replicates. However, ancestor NOT-NAND performs the NOT task first and ancestor NAND-NOT performs the NAND task first. While we depict the tasks as

Task	Risk Treatments			
	NOT risky	NAND risky	No risk	Both risky
NOT	25%	0%	0%	25%
NAND	0%	25%	0%	25%

Table 1: The four risk treatments for a two-task environment. The rows describe the lethality risks associated with tasks NOT and NAND. (E.g., A 25% risk means that while performing the task, the organism has a 25% chance of dying.) The columns describe a specific treatment.

atomic units within this Figure to denote order, to actually perform a task an organism must execute several instructions. By varying the ancestor organism, we are able to verify that any patterns of temporal polyethism result from the riskiness associated with the tasks, not the initial genomic structure of the organisms. For each ancestor, we performed all four risk treatments. If task riskiness is a sufficient pressure to result in temporal polyethism, then we should see that organisms evolve to perform the less risky task first and the more risky task second, regardless of whether NOT or NAND is the risky task, and the initial order of the tasks with the ancestor organism's genome.
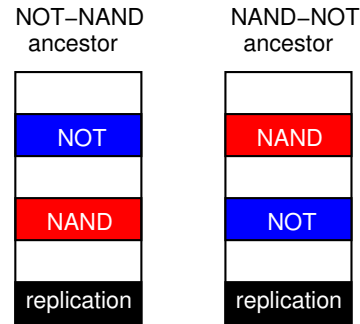

Figure 1: The layout of the ancestor organisms for two-task temporal polyethism experiments. The NOT-NAND ancestor performs task NOT, performs task NAND, and then replicates. The NAND-NOT ancestor performs task NAND, performs task NOT, and then replicates. Because the genomes are circular, after each organism replicates, it resumes execution at the top of its genome.

Figures 2 and 3 depict the results of the experimental treatments. For all results, the mean age at which a task is performed includes the age of organisms who died attempting to perform that task. Figure 2 depicts the treatments in which task NOT is risky. In both treatments that vary the ancestor organism, the mean age at which NOT is performed is significantly greater than the mean age at which NAND is performed (Mann-Whitney U Test). For example, for the NOT-NAND ancestor, NOT is performed at the mean age of 750.37 ± 27.45 cycles and NAND is performed at the mean age of 453.43 ± 29.12 cycles. The treatment seeded with the

NOT-NAND ancestor reversed the order in which the tasks were performed in 26 out of 30 replicates. Additionally, 23 out of 30 replicates seeded with the NAND-NOT ancestor performed the riskier task NOT at a later age than task NAND.

Figure 3 depicts the treatments where task NAND is risky. For both treatments, the mean age at which NAND is performed is significantly greater than the mean age at which NOT is performed (Mann-Whitney U test). 27 out of 30 replicates with the NOT-NAND ancestor and 28 out of 30 replicates with the NAND-NOT ancestor performed the riskier task NAND at a later age than task NOT. These treatments support our hypothesis that task riskiness can result in temporal polyethism in which the more risky task is performed later in the lifetime of the organisms.
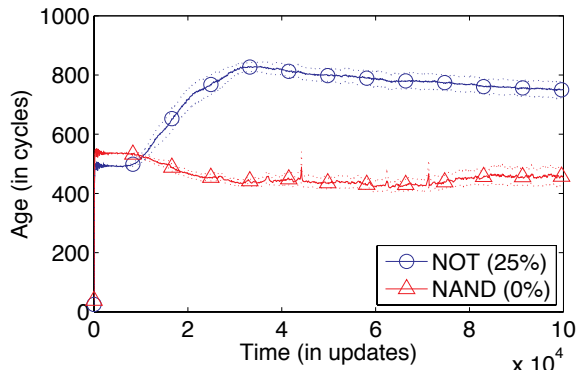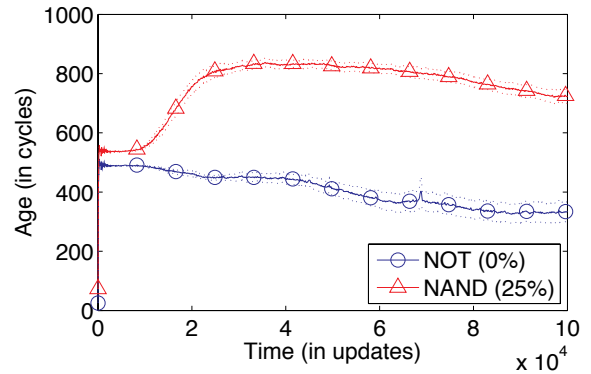

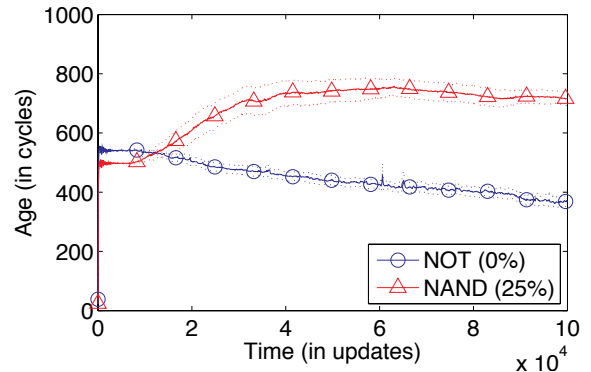(a) Ancestor: NOT-NAND; Treatment: NOT is risky
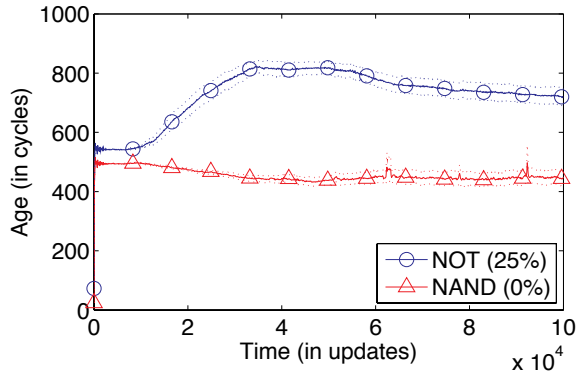
(b) Ancestor: NAND-NOT; Treatment: NOT is risky

Figure 2: Task ordering over time in treatments where task NOT is risky compared across different ancestors. For each plot, the x-axis is evolutionary time and the y-axis is the mean age in cycles when the associated task is performed. Dotted lines represent standard error. Task NOT is consistently performed later in the lifetime of the organisms, regardless of the starting order.

Figures 4 and 5 depict the results of our controls, which are designed to verify that, given the same level of risk, there is nothing inherent in the tasks that results in one being per-

(a) Ancestor: NOT-NAND; Treatment: NAND is risky

(b) Ancestor: NAND-NOT; Treatment: NAND is risky

Figure 3: Task ordering over time in treatments where task NAND is risky compared across different ancestors. For each plot, the x-axis is evolutionary time and the y-axis is the mean age in cycles when the associated task is performed. Dotted lines represent standard error. Task NAND is consistently performed later in the lifetime of the organisms, regardless of the starting order.

formed earlier or later in the organisms' lifetimes. Figure 4 depicts the results of the control treatments in which neither task is risky. For these control treatments, the average age at which organisms perform tasks increases over the duration of the experiment. This change results from individual organisms evolving to perform the same task multiple times within their lifetime resulting in the average age of task performance increasing. However, the mean age at which task NOT is performed is not significantly different than the mean age at which task NAND is performed (Mann-Whitney U Test). Figure 5 depicts the results of the control treatments in which both tasks are risky. For both treatments, the mean age at which the organisms perform the tasks reflects their order in the genome. One thing to note about this control is that the high level of risk associated with both tasks decreases the rate of colony replication. In fact, many colonies lost the ability to replicate altogether and survived merely because other colonies within their trial were also unable

to replicate. Thus, these colonies are not actually evolving in an adaptive fashion. However, the data provided by the controls indicate that there is nothing inherent in the NOT or NAND tasks that implies an ordering. Taken together, these treatments indicate that more risky tasks are, on average, performed later within the lifetime of the organisms.

(a) Ancestor: NOT-NAND; Treatment: No risk

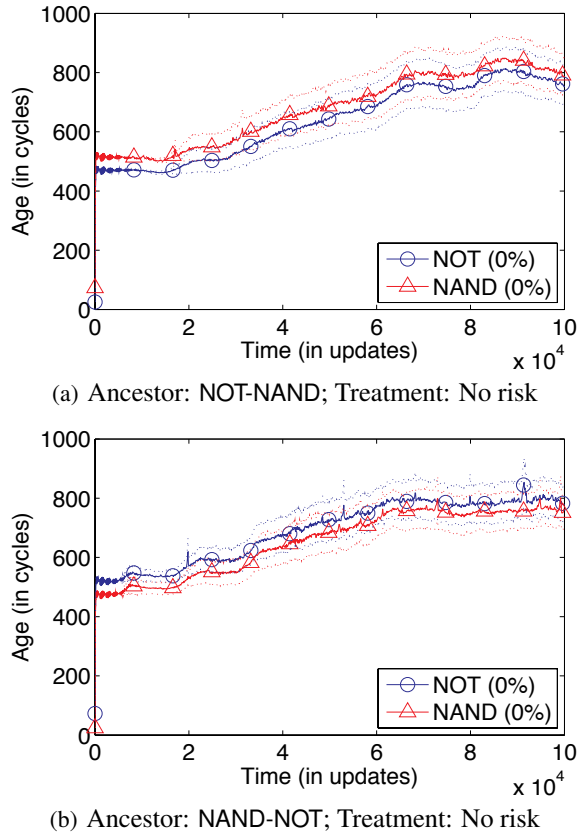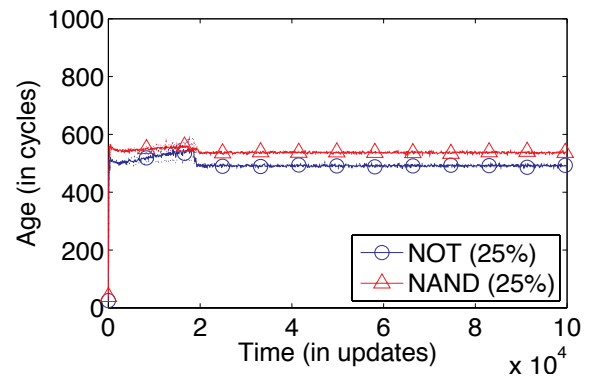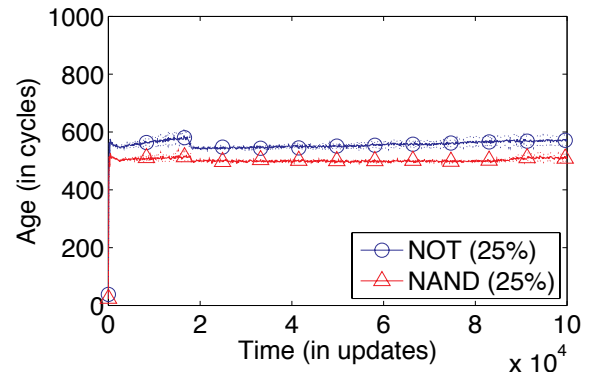(b) Ancestor: NAND-NOT; Treatment: No risk

Figure 4: Task ordering over time in control treatments where neither task is risky. For each plot, the x-axis is evolutionary time and the y-axis is the mean age in cycles when the associated task is performed. Dotted lines represent standard error. In these results, the controls indicate that there is nothing intrinsic about the tasks that is driving the temporal polyethism results.

To better understand how the colonies were responding to the amount of risk associated with a task, we performed several additional treatments in which we set the lethality risk for the risky task to 7%, 15%, and 20%. For these new risk conditions, we again varied the ancestor and also which task was risky. Figure 6 shows the number of replicates out of 30 that evolved a temporal polyethism pattern, where the more risky task was performed later in life. For all risk levels, if the ancestor organism had properly ordered the tasks (i.e., it performed the risky task last), then most replicates were able to maintain the temporal polyethism pattern. For example, when NOT is the risky task, most replicates with

(a) Ancestor: NOT-NAND; Treatment: All risky

(b) Ancestor: NAND-NOT; Treatment: All risky

Figure 5: Task ordering over time in control treatments where both tasks are risky. For each plot, the x-axis is evolutionary time and the y-axis is the mean age in cycles when the associated task is performed. Dotted lines represent standard error. In these results, the controls indicate that there is nothing intrinsic about the tasks that is driving the temporal polyethism results.

the ancestral organism NAND-NOT maintained the ordering present in the ancestor genome and performed NOT later in life. However, these data also reveal that at lower risk levels, fewer replicates were able to evolve the temporal polyethism pattern if the ancestral organism started with the riskier task being done earlier in life. For example, fewer replicates with the ancestral organism NOT-NAND were able to rearrange their genomes such that the risky task NOT was done later in life when the lethality risk was lower. These results indicate that the level of risk plays an important role in the evolution of temporal polyethism.

Analyses

We have demonstrated that colonies evolve to perform more risky tasks, on average, later within their lifetime than safe tasks. Next, we examine how this behavior interacts with reproduction and then conduct a case study analysis of a colony that exhibits this behavior.

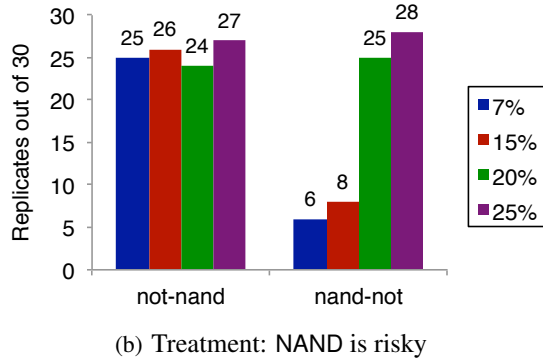(a) Treatment: NOT is risky
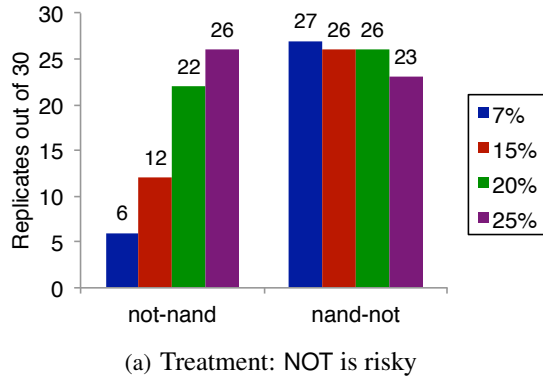

(b) Treatment: NAND is risky

Figure 6: The results of the temporal polyethism treatments, where risk level was varied. The y-axis of both plots is the number of replicates out of 30 that were able to do the risky task later in life. The x-axis shows the results from two different ancestors: NOT-NAND and NAND-NOT. (a) shows results from when NOT is the risky task and NAND does not have any risk. (b) shows results from when NAND is the risky task and NOT does not have any risk. The key denotes the lethality risk for the risky task.

Task Performance and Replication. Within these experiments, organisms have a pressure not just to perform tasks, but also to replicate and produce clones capable of performing these same tasks. One topic we were interested in exploring is when the organisms replicated. To address this topic, we examined a case study treatment from our original two-task experiment that begins with the NOT-NAND ancestor and in which task NOT is risky. Figure 7 depicts the mean age at which the tasks were performed and at which the organisms replicated. Intriguingly, the organisms performed the less risky task (NAND), replicated, and then much later in their life performed the more risky task (NOT). In this example, this result suggests that the organisms have evolved a strategy that balances their need to perform tasks, the risk associated with these tasks, and their need to replicate.

Two-Task Colony Case Study. Next, we examined the behavior of a successful colony from our two-task experi-
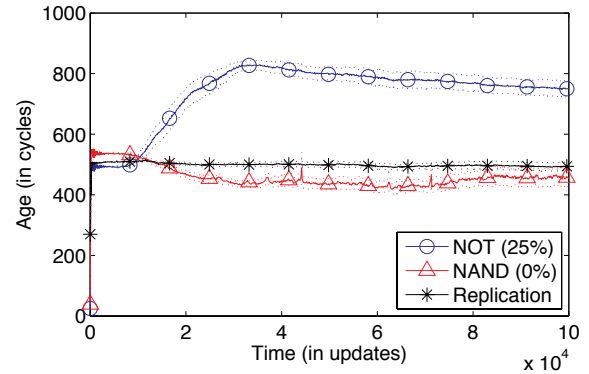

Figure 7: These results depict the mean age at which task NOT (blue line with circles), task NAND (red line with triangles) and replication (black line with stars) are performed for the case study treatment where NOT is risky and the runs were started with the NOT-NAND ancestor. These results suggest that the organisms are performing task NAND one or more times, replicating, and then performing task NOT.

ment that begins with the NOT-NAND ancestor and in which task NOT is risky to ascertain how it managed task performance and replication (results depicted in Figure 2a). The organisms within this colony executed a precise behavioral plan that is depicted in the phenotype portion of Figure 8. They performed task NAND, replicated, performed task NAND again, replicated again, and then repeatedly performed task NOT (the risky task) until it killed them. The organisms in this case study clearly exhibit the temporal polyethism pattern of performing the risky task after their other duties had been completed.
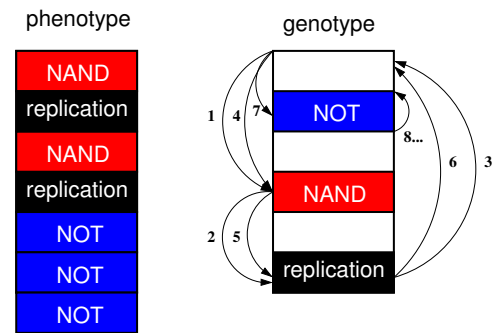

Figure 8: Diagrams of the phenotype (left) and genotype (right) of a case study organism whose colony exhibited temporal polyethism with two tasks. The numbered arrows surrounding the genotype indicate the order in which instructions were executed to produce the phenotype. In this case, the genotype is very similar to the NOT-NAND ancestor. The risk-based order in which the tasks were performed depended upon control-flow instructions in the genome.

A second topic we explored was how the genome archi-

tecture of this case study supported this behavior. For example, organisms may have rearranged their genome to support task ordering (i.e., by moving the instructions that performed more risky task to the end of their genome) or organisms may have evolved to use control-flow instructions that enable them to skip over portions of their genome. In this case, the organisms evolved to use the control-flow instructions. The architecture of the genome, which is depicted in the genotype portion of Figure 8, is extremely similar to the ancestor organism: task NOT is encoded first, then task NAND, and lastly replication. However, the organisms evolved to have both jump instructions (to skip task NOT until the remainder of the genome had been executed twice) and a loop to continue to perform task NOT until death. Organisms set and used the value of a register that was preserved during replication to track which genome iteration they were on and to modify their behavior accordingly. The numbered arrows in Figure 8 depict the order in which the elements of the genome were executed.

Measuring Temporal Polyethism. There are two challenges associated with measuring temporal polyethism: First, each organism may perform each task multiple times over its lifetime. Second, an organism may die while performing a task as either the consequence of the lethality risk associated with that task or as the result of being replicated over by a neighboring organism. Thus far, to measure temporal polyethism, we have examined the mean age at which organisms perform a task. Here we assess this measurement by comparing it to two other potential measurements: (1) the mean age at which the organisms *first* perform a task, and (2) the mean age at which the organisms perform a task when all lethality risks are removed from the system.

For this analysis, we used the case study colony whose genotype and phenotype are depicted in Figure 8. The results of the three measurements are shown in Table 2. All three measurements provide similar results for the age of the non-risky task (NAND). The results vary for the risky task. Specifically, the mean first age for task NOT (964) is substantially less than the mean age (1103.78), which, in turn, is substantially less than the mean age without lethality (1515.02). However, all three measurements capture the temporal polyethism structure in which task NAND is performed much earlier than task NOT within an organism's lifetime.

Discussion

In this paper, we have described how we have used Avida to explore a set of evolutionary conditions that give rise to temporal polyethism, a division of labor pattern. Specifically, we found that assigning different lethality risks to various types of tasks was a sufficient pressure to produce a temporal polyethism pattern, where organisms performed the least risky task earlier in their lifetime and then switched

Measurement	NOT	NAND
Mean Age	1103.78±25.93	236.43±5.69
Mean First Age	964±0	232.90±4.28
Mean Age No Lethality	1515.02±58.71	215.89±9.02

Table 2: Three different measurements of the age at which organisms perform a task. While all three have similar results for the non-risky task (NAND), the results differ a bit more for the risky task (NOT). However, all three measurements report a highly significant and substantial difference in mean ages between the two tasks and thus capture the temporal polyethism structure.

to performing the more risky task at the end of their life. This strategy balances a colony's need to maintain members of the colony and also to complete risky tasks. As such, this temporal polyethism structure enables the colony to be more efficient at gathering resources by having older organisms complete riskier tasks when they are closer to dying. In our analyses, we found further evidence that organisms made use of control flow instructions and genomic architecture modifications to achieve this behavior.

While our study sheds light on the evolutionary pressures that can give rise to a temporal polyethism pattern, the proximate mechanisms employed by colonies to exhibit this pattern could rely on either spatial structure (as proposed by the foraging for work hypothesis) or developmental hormones regulated by aging (as proposed by the task-riskiness hypothesis). For example, since the spatial structure of the nest corresponds with the riskiness of tasks, organisms may employ a foraging for work mechanism to achieve this pattern. Thus, workers may start within the nest taking care of the brood and then progress outward to more risky tasks, such as guard, undertaker, or forager (Hölldobler and Wilson, 2009). Even within Tofts' foraging for work model, workers switch between tasks based on colony need, and riskier tasks on the outside of the nest are a constant draw for work, trapping older workers outside of the nest (Tofts, 1993; Robson and Beshers, 1997).

Task switching may also be regulated by age using a variety of developmental hormones. Juvenile hormone (JH) is considered a mediator for temporal polyethism in advanced eusocial insects and even in some primitive wasps (Robinson, 1987; Shorter and Tibbetts, 2009; Sullivan et al., 2000). Studies of honeybees and some species of wasps show that when workers were treated with JH, they transitioned from nursing to foraging earlier in life (Robinson, 1987; Shorter and Tibbetts, 2009; Sullivan et al., 2000). In particular, honeybees have higher concentration of JH when they are older and foraging than they do when they are younger and taking care of the brood (Shorter and Tibbetts, 2009). Knocking down vitellogenin, a gene associated with JH, in bees similarly results in earlier task switching to foraging and shorter lifespans (Nelson et al., 2007). This example highlights

how developmental genes can regulate the performance of risky tasks so that they are done later in life and increase worker bee longevity. This proximate mechanism is compatible with the evolutionary pressures associated with ordering tasks according to risk.

An additional pressure that may reinforce ordering the performance of tasks according to risk is the benefit of conserving viable reproductives within the colony. In species in which workers have the option of reproducing when the queen dies, younger workers may have viable eggs and higher reproductive success than older sisters. By having younger workers perform safer tasks within the nest, the colony as a whole preserves its reproductive potential (Sendova-Franks and Franks, 1993).

Within this study, we have demonstrated that associating tasks with lethality risks is sufficient for evolving a temporal polyethism pattern. In the future, we will explore the effect of adding additional tasks and levels of risk. In addition, we will add in task-switching costs to address a limitation of Tofts' model, which assumes (unrealistically) that workers can switch between tasks without any delays. The evolutionary conditions leading to the rise of temporal polyethism is an important step in understanding the division of labor patterns we see in eusocial insects.

Acknowledgements

References

Crespi, B. J. (2001). The evolution of social behavior in microorganisms. *Trends in Ecology & Evolution*, 16(4):178–183.

Duffy, J. E. (2003). The ecology and evolution of eusociality in sponge-dwelling shrimp. In *Genes, Behaviors and Evolution of Social Insects*. Hokkaido University Press.

Franks, N. R., Tofts, C., and Sendova-Franks, A. B. (1997). Studies of the division of labour: neither physics nor stamp collecting. *Animal Behaviour*, 53(1):219 – 224.

Goldsby, H. J., Dornhaus, A., Kerr, B., and Ofria, C. (2012). Task-switching costs promote the evolution of division of labor. In *preparation*.

Hölldobler, B. and Wilson, E. O. (2009). *The superorganism: the beauty, elegance, and strangeness of insect societies*. WW Norton & Company.

Jandt, J. M. and Dornhaus, A. (2009). Spatial organization and division of labour in the bumblebee bombus impatiens. *Animal Behavior*, 77:641–651.

Knoester, D. B., McKinley, P. K., Beckmann, B., and Ofria, C. (2007). Directed evolution of communication and cooperation in digital organisms. In *Proceedings of the European Conference on Artificial Life (ECAL)*.

Lenski, R. E., Ofria, C., Pennock, R. T., and Adami, C. (2003). The evolutionary origin of complex features. *Nature*, 423:139–144.

Nelson, C., Ihle, K., Fondrk, M., Page, R., and Amdam, G. (2007). The gene vitellogenin has multiple coordinating effects on social organization. *PLoS biology*, 5(3):e62.

Ofria, C. and Wilke, C. O. (2004). Avida: A software platform for research in computational evolutionary biology. *Journal of Artificial Life*, 10:191–229.

Pike, N. and Foster, W. A. (2008). *Ecology of Social Evolution*. Springer Berlin Heidelberg.

Queller, D. C. and Strassmann, J. E. (2003). Eusociality. *Current Biology*, 13(22):R861–863.

Robinson, G. (1987). Regulation of honey-bee age polyethism by juvenile-hormone. *Behavioral Ecology and Sociobiology*, 20(5):329–338.

Robson, S. K. and Beshers, S. N. (1997). Division of labour and 'foraging for work': simulating reality versus the reality of simulations. *Animal Behaviour*, 53(1):214–218.

Seeley, T. D. (1982). Adaptive significance of the age polyethism schedule in honeybee colonies. *Behavioral Ecology and Sociobiology*, 11(4):287–293.

Sendova-Franks, A. and Franks, N. R. (1993). Task allocation in ant colonies within variable environments (a study of temporal polyethism: experimental). *Bulletin of Mathematical Biology*, 55(1):75–96.

Shorter, J. and Tibbetts, E. (2009). The effect of juvenile hormone on temporal polyethism in the paper wasp polistes dominulus. *Insectes sociaux*, 56(1):7–13.

Sullivan, J. P., Jassim, O., Fahrbach, S. E., and Robinson, G. E. (2000). Juvenile hormone paces behavioral development in the adult worker honey bee. *Hormones and Behavior*, 37(1):1–14.

Tofilski, A. (2002). Influence of age polyethism on longevity of workers in social insects. *Behavioral Ecology and Sociobiology*, 51:234–237. 10.1007/s00265-001-0429-z.

Tofts, C. (1993). Algorithms for task allocation in ants.(A study of temporal polyethism: theory). *Bulletin of Mathematical Biology*, 55(5):891–918.

Traniello, J. F. and Rosengaus, R. B. (1997). Ecology, evolution and division of labour in social insects. *Animal Behaviour*, 53(1):209–213.

Wilson, E. O. (1980). Caste and Division of Labor in Leaf-Cutter Ants (Hymenoptera: Formicidae: Atta): I. The Overall Pattern in *A. sexdens*. *Behavioral Ecology and Sociobiology*, 7(2):143–156.