

The Evolution of Temporal Polyethism

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Abstract

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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 thesis, 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. When we associate the two different tasks with different lethality risks, 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. In trials with three tasks, evolution produces a genome in which the tasks are reordered such that the mean age of completion of the riskiest task is later in life in the majority of the trials. These results demonstrate that pressures resulting from the relative riskiness of various tasks is sufficient to favor the evolution of temporal polyethism. Our preliminary results indicate that when there are competing pressures of lethality risks associated with tasks versus task-switching costs (a penalty to transition between tasks) to organisms, we see that temporal polyethism is still favored as a division-of-labor strategy.

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Chapter 1

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 [2, 3, 11, 12, 19, 30]. 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 [12]. Moreover, many eusocial organisms, such as leaf-cutter ants [30], bumblebees [12], and aphids [18], 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 [12]. It is important to understand how a complex biological system can arise with the successful integration of balancing the colony's needs with the needs of an individual.

1.1 *Temporal polyethism*

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 [4, 11, 22, 24, 26, 27, 28]. 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 [23]. Within ant colonies, a similar shift is performed from activities within the nest, such as brood care, to foraging activities outside the nest [11]. Researchers are still actively exploring the causes and mechanisms underlying this division-of-labor pattern. In the following chapters, we explore 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 [11, 22, 28]. 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 [11]. For example, tasks that are performed inside of a colony (ie. taking care of the brood) are safer than tasks performed outside of the colony. Foraging, a task commonly responsible for the loss of 1% to 10% of the colony population per day [11], is performed when the organism is older and more likely to die of natural age-related causes. In this sense, the worker is more expendable to the colony, and therefore, the colony optimizes the use of its workers. [26]. In contrast, the *foraging-for-work* hypothesis assumes that as organisms are born, they perform tasks closest to them and proceed to perform tasks farther from the center of the nest [4, 11, 24, 27]. This explanation depends only upon organisms' reactive responses to task stimuli. The 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 [4, 11, 22, 28]. Specifically, studies with monomorphic ants provide evidence that supports the foraging-for-work hypothesis, indicating 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 [24]. 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 [24]. In this situation, young sisters stay near the brood and replicate because they have more viable eggs, and older workers do more tasks and are faithful to the profitable employment that they find at the time.

In the original foraging-for-work mathematical model created by Tofts [27], workers are born into the brood pile, which is in the center of the colony, and ants change tasks when work was unavailable at the current location. Individuals start to move outward as they actively see out work; however, they will stay at a position if there is still work to be done in that location. Workers are allocated to tasks without reference to their age, and their movement between tasks is similar to a production line as tasks are spatially ordered and

sequential.

Tofts' model does have many critics. One critique highlights that the way in which workers can move between tasks creates a biologically unrealistic colony as workers can move in any direction [22]. In particular, both ends of the production line have unlimited amounts of work—the brood side has an infinite amount of work and the foraging side always can give work to those requesting it [27]. Yet, realistically, ants are not likely to take care of the brood after they go out of the colony and forage [22]. In this sense, the foraging-for-work hypothesis is undirectional, and therefore, unrealistic.

Tofts' model also has been criticized for being overly specific to explain division of labor from the eucosial *Hymenoptera* to the naked mole rats [22]. Tofts' model highlights that there is a correlation between a worker's age and the task that it completes, but this relationship is emergent and not causal [27]. However, the model overlooks termites (order *Isoptera*) which have many similarities in sociality to the eusocial *Hymenoptera* [28]. Higher orders of termites have a well-developed age-related division-of-labor strategy that has been said not to have arisen from a foraging-for-work strategy but rather as a result of other evolutionary factors, such as nest stability and worker sterility [28]. Key critiques of Tofts' model note that the model does not account for evolutionary pressures that could lead to different forms of temporal polyethism in different species [28].

In addition, an alternative mathematical model was created by Tofilski with a set of two tasks that each had different mortality rates [26] - one “safe” task and one “risky” task. Workers have a fixed amount of resource usage for life; for example, organisms can only do the two tasks a certain number of times in their lifetime. The higher the expenditure of resources, the shorter the lifespan on the worker. Fitness is based on the longevity of workers, and workers do not reproduce. The mathematical model tests the difference in longevity of workers in two scenarios. In the first, workers alternate between tasks, ABABAB, etc., (A being the safe task and B being the risky task) to emulate a colony in which workers do tasks without taking into account riskiness. In the second, Tofilski applies a temporal polyethism model of doing one task earlier in life and then the other task later in life as such AAABBB. He shows that longevity of workers in a colony that performs tasks without regard to the amount of risk associated with them (the first scenario) is significantly lower

than the longevity of workers in colonies that have that perform riskier tasks later in their lives (the second scenario) in accordance with the task-riskiness hypothesis. Tofilski argues that it is more beneficial for a colony to divide labor such that older workers do riskier tasks if antagonistic pleiotropy and accumulation of deleterious mutations are taken into account.

There are many studies that provide evidence for a causal relationship between the task a worker performs and the worker's age [11, 22, 28]. There have been many studies on genetic and hormonal changes according to age that influence the task the worker completes [1, 15, 17, 20, 21, 25]. Juvenile hormone (JH) regulates temporal polyethism in many eusocial insect species. In particular, treating wasps from *Polistes dominulus*, a species that has age-related division of labor, with juvenile hormone will accelerate their task switching to foraging earlier in their life [25]. Research with *Polistes* shows that foraging time increases with workers' age [25]. Similar results were seen when honeybees were treated with JH in that they also became precocious foragers [21]. In addition, honeybees also had an increased sensitivity to alarm pheromones to protect the hive when under attack [21, 20]. In response to a brick dropped on a honeybee hive, it was observed that the only older bees defensively responded to protect the hive [1]. However, Franks and Tofts counter that this may result from spatiality in that older bees are closest to the outside and therefore, more ready to respond [5]. A similar effect was seen for bees turning into precocious foragers when older bees in the colony were removed [17]. When the oldest workers are taken out of the colony, the eldest remaining workers transition to foraging even if it is early for their age [17]. The underlying explanation for this phenomena is that the next set of oldest workers are the most expendable for the colony, and therefore, it is beneficial for the colony for them to transition into the most risky task for the colony. Interestingly, when the youngest workers are removed from the colony, there is a similar transition for foragers with the least experience to revert back to less-risky larval-care tasks [17]. These observations contrast with Tofts' assertions that there is no causal relationship between age of a worker and the task a worker attempts. The age-related hormonal aspects of task-switching make a case for tasks not being correlated with chronological age per se but instead physiological age [21]. In a sense, there is a dual plasticity as physiology and environmental stimuli both play a role in what task is performed.

There is evidence for both the task-riskiness hypothesis and the foraging-for-work hypothesis [23, 29]. In the *Pheidole dentate* and *Camponotus floridanus* species of ants, it has been observed that there is both age and spatial organization with minimal travel between tasks [23, 29]. In honeybees, there is a compromise between competing pressures of performing tasks and locating the tasks [23]. The time it takes to switch between tasks and find the next task is a cost on both the worker and the colony as a whole. While it may be the case that workers specializing on a particular task may increase task performance, specialization may inhibit colonies from being flexible when work is needed in other areas. As such, it is possible that workers become “semi-specialists” in that they do a set of tasks at particular age ranges [23]. Temporal polyethism has to balance the need to have the most expendable workers do the riskiest tasks, have successful task performance, and maintain the ability to adapt to environmental perturbations [29].

1.2 Approach

As Hölldobler and Wilson state, “Each species has its own distinctive pattern of temporal polyethism” [10]. While many studies have examined potential proximate causes of temporal polyethism exhibited by current eusocial colonies [1, 11, 15, 17, 20, 21, 22, 25, 28], it is challenging to explore the evolutionary conditions that may give rise to this pattern. Both field observations of evolution and experimental studies of evolution in lineages of natural 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 [16]. Each digital organism has a virtual CPU, a genome (a circular list of computer instructions), and coordinates for their location in the environment as seen in Figure 1.1. The virtual CPU of an organism consists of three general-purpose registers (indicated by AX, BX, and CX in Figure 1.1) and two stacks. Each digital organism executes instructions on its virtual CPU. The instruction set in Avida is Turing-complete and allows for basic computational tasks, such as addition, multiplication, and bit-shifts, controlling the execution flow and self-replicating. An organism performs logic operations (NOT, NAND,

etc.) called *tasks* by executing the instructions in their genome. Task completion enables organisms to collect resources from the environment, which in turn rewards them with faster execution of instructions on their virtual CPU in relation to other organisms in the population. This allows for organisms to compete with their neighbors. Avida meets all of the requirements for evolution: variation, heritability, and differential fitness. Avida has previously been used to study topics such as division of labor [7], origin of complex features [14], and evolution of cooperation [13]. Digital organisms have rapid generation times (e.g., thousands of generations in a few hours).

1.3 Avida

Figure 1.1 depicts an Avida population where colors represent different genotypes and the structure of an individual organism.

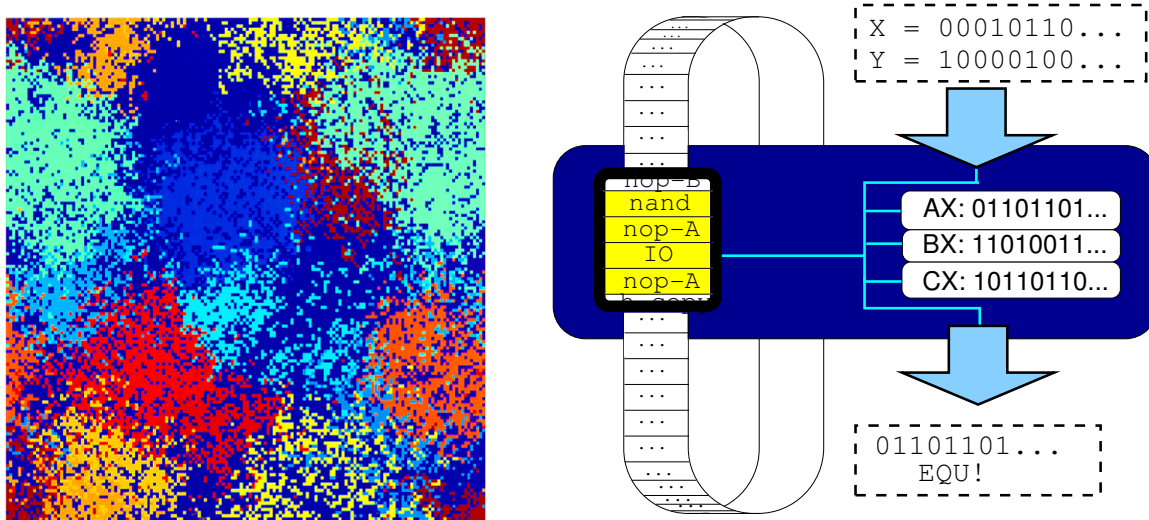


Figure 1.1: Left: An Avida population containing multiple genotypes in a spatial environment, where different colors indicate organisms with different genotypes. Right: The structure of an individual organism, including its genome, input, internal registers, and output.

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. In order 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 in a eusocial insect colony, 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 modified Avida to associate each task with a *lethality risk* that specifies the probability of the organism dying while attempting to complete the task. Non-risky (or safe) tasks have a lethality risk of 0, and the 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, colonies are seeded with an *ancestor* organism that performs all the types of tasks necessary to contribute to the requirements for colony replication. 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 takes an average organism to execute 30 *cycles* – each instruction takes one cycle to execute.

We explicitly removed any spatial component to task performance to determine whether temporal polyethism could be explained without reference to space, instead, the risk associated with tasks as discussed in Chapters 2 and 3. In Chapter 4, we add in task-switching costs to penalize organisms from switching between tasks in order to determine the outcome of competing pressures of risks associated with tasks as well as penalties associated with switching between tasks.

1.4 Thesis statement

In response to task-associated lethality pressures, the organisms evolved division of labor strategies in which tasks associated with less risk were done earlier in an organism's life and riskier tasks were performed later in life. These data provide support for the hypothesis that risks associated with aging and various tasks are sufficient to produce temporal polyethism.

Chapter 2

TEMPORAL POLYETHISM WITH TWO TASKS

In this chapter, we look at the simplest case to examine the evolution of temporal polyethism. We start with organisms that can do only two tasks, and we observe if they can rearrange these two tasks when risks are associated with them [6, 8].

2.1 Experimental setup

We examine whether the risks associated with aging and tasks are sufficient to evolve temporal polyethism in colonies of organisms. We started by making an environment in which colonies had to perform two tasks (NOT and NAND) 250 times each in order for the colony to replicate. In Table 2.1, we describe the four risk treatments that had varied 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).

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

Table 2.1: The four risk treatments for the two-task environment. The rows describe the lethality risks associated with tasks NOT and NAND. A 25% risk means that while performing the task, the organism has a 25% chance of dying. The columns describe a specific treatment.

Additionally, we created two possible ancestor organisms (depicted in Figure 2.1). Each ancestor has the ability to complete each task once and then self-replicate. However, ancestor NOT-NAND performs the NOT task first and ancestor NAND-NOT performs the NAND task first. By changing 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. We performed all four risk treatments for each ancestor organism. If our hypothesis is correct and task riskiness is a sufficient pressure to result in temporal polyethism, then we should see that organisms perform the less risky task first and the more risky task second, regardless of whether NOT or NAND is the risky task of the tasks in the ancestor organism’s genome. The mean age at which a task is performed includes the age of organisms who died attempting to perform that task.

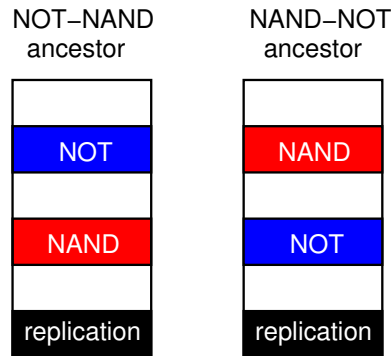


Figure 2.1: The genome layout of the ancestor organisms for two-task temporal polyethism experiments. The NOT-NAND ancestor performs task NOT, performs task NAND, and then replicates. The NAND-NOT ancestor performs task NAND, performs task NOT, and then replicates. Because the genomes are circular, after each organism replicates, it resumes execution at the top of its genome.

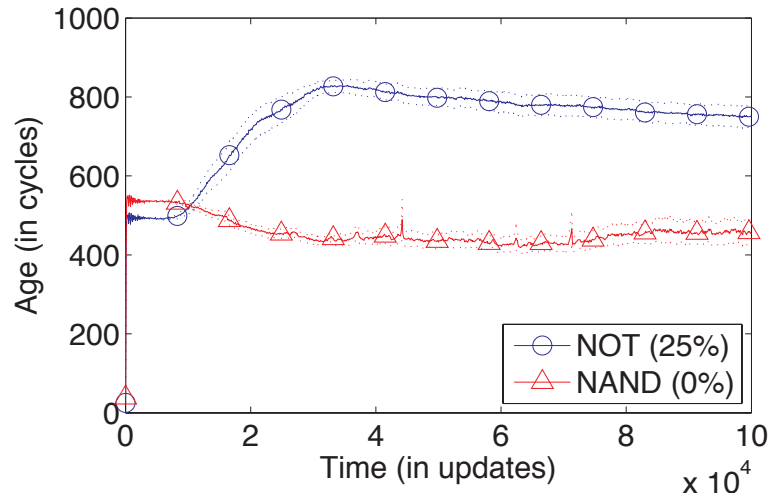
2.2 Two-task results

Figures 2.2 and 2.3 depict the results of the experimental treatments. Figure 2.2 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, $p < 0.05$). 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

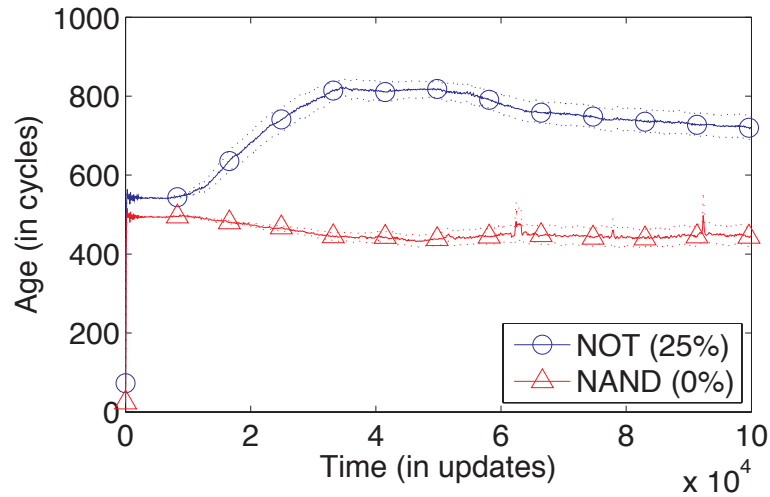
at a later age than task NAND.

Figure 2.3 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, $p < 0.05$). 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. 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.

Figures 2.4 and 2.5 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 performed earlier or later in the organisms' lifetimes. Figure 2.4 depicts the results of the control in which neither task is risky. For this control, 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 over the duration of the experiment. 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, $p > 0.05$). Figure 2.5 depicts the results of the control 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 group 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: NOT is risky



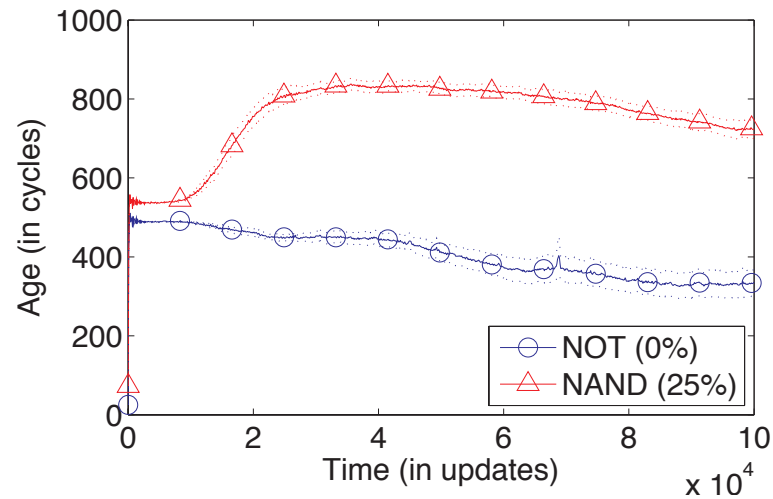
(b) Ancestor: NAND-NOT; Treatment: NOT is risky

Figure 2.2: 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, no matter the starting order.

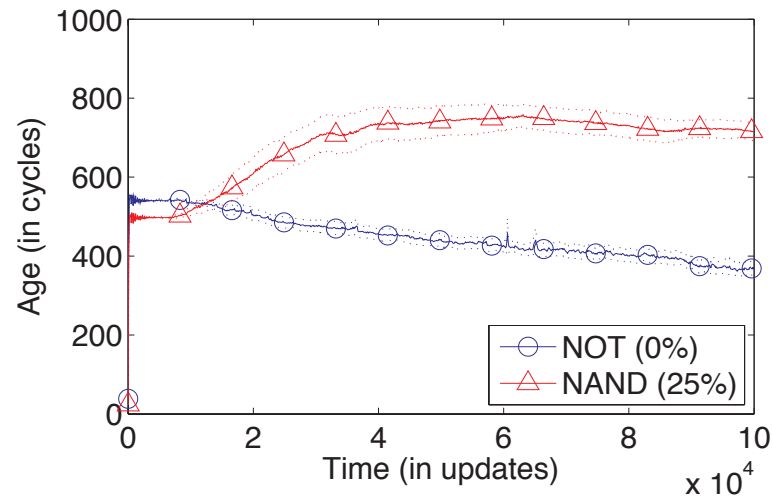
2.3 Varying risk levels

2.3.1 One safe task and one risky task

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



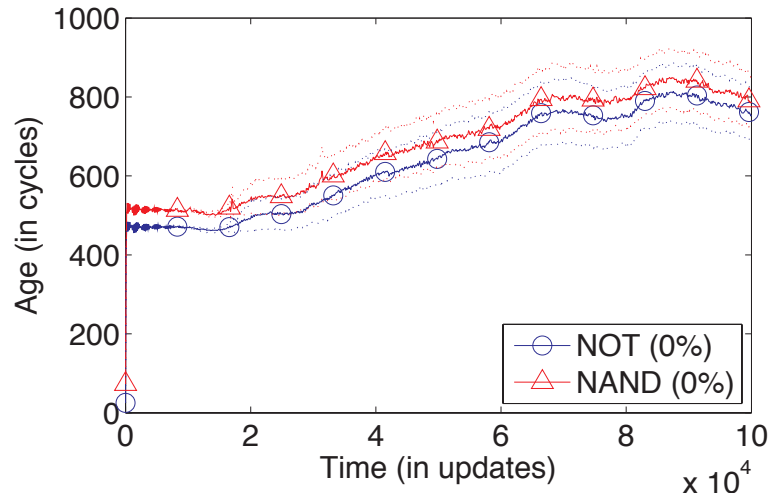
(a) Ancestor: NOT-NAND; Treatment: NAND is risky



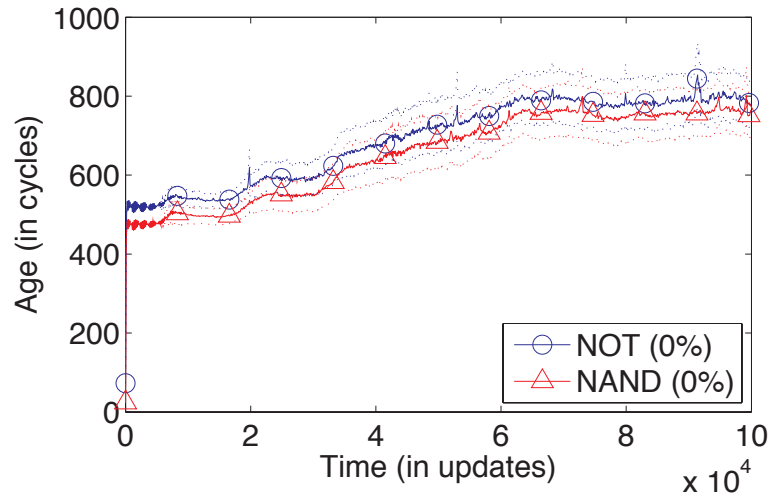
(b) Ancestor: NAND-NOT; Treatment: NAND is risky

Figure 2.3: 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, no matter the starting order.

to 7%, 15%, and 20%. For these new risk conditions, we again varied the ancestor and also which task was risky. Figure 2.6 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



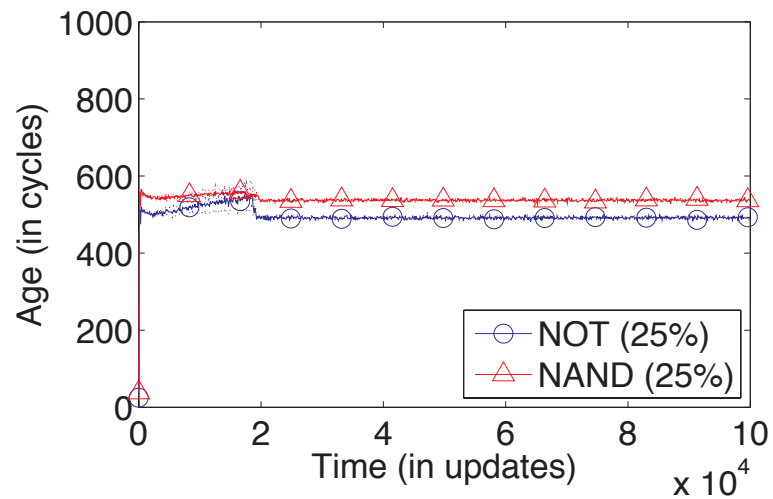
(a) Ancestor: NOT-NAND; Treatment: No risk



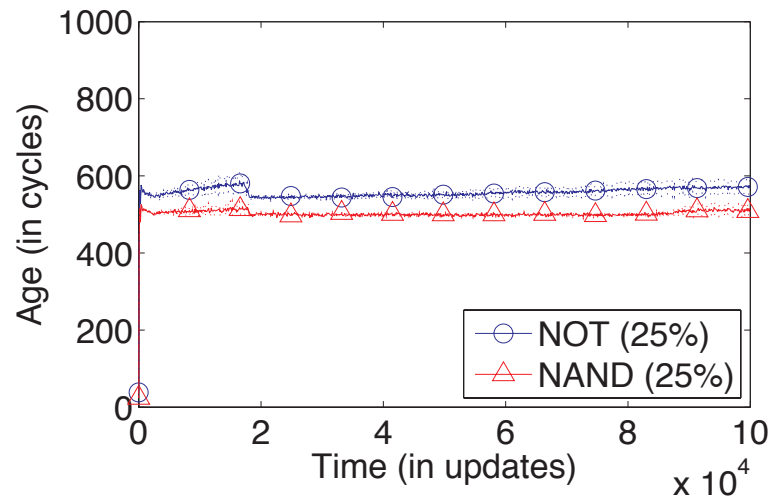
(b) Ancestor: NAND-NOT; Treatment: No risk

Figure 2.4: 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.

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 the ancestral organism NAND-



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

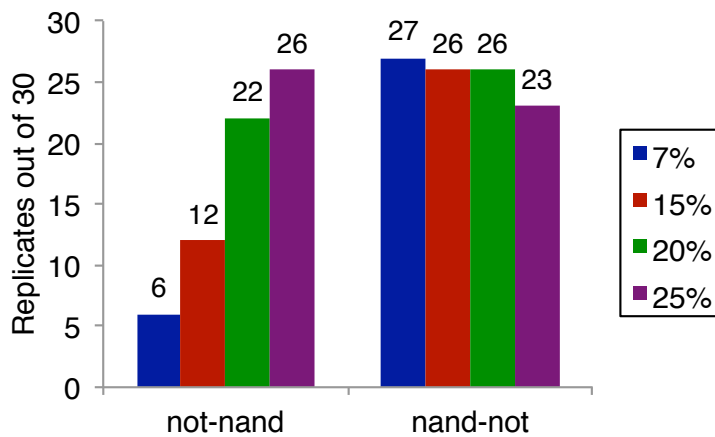


(b) Ancestor: NAND-NOT; Treatment: All risky

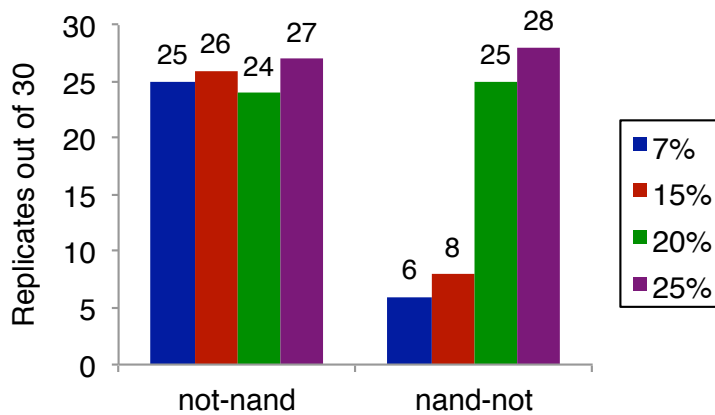
Figure 2.5: Task ordering over time in control treatments where both tasks are risky. For each plot, the x-axis is evolutionary time and the y-axis is the mean age in cycles when the associated task is performed. Dotted lines represent standard error. In these results, the controls indicate that there is nothing intrinsic about the tasks that is driving the temporal polyethism results.

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.



(a) Treatment: NOT is risky



(b) Treatment: NAND is risky

Figure 2.6: 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.

2.3.2 *Two risky tasks*

In this section, we look at how colonies respond if they have to complete two tasks that have differing levels of lethality. Can colonies evolve such that they do the riskiest task later in life if both tasks have lethality risks associated with them? In our previous experiments, if the ancestral organisms can complete the task with 25% lethality first, they transition to the safe task that cannot kill them. In this case, if an organism completes the safe task first and then dies while attempting to complete the risky task, the colony as a whole has a net gain of the safe task. As colonies have the same number of required tasks for both the safe and risky tasks, this would result in a surplus of the safe task before the colony can complete enough of the risky task in order to replicate. Therefore, there would not be as much of a pressure to evolve a pattern where the riskier task is done later in life if the ancestor does not already have this pattern. Organisms that complete the riskier task will almost always be able to complete the safe task (unless there have been mutations to alter this). To address this concern, the lethality risks of the two tasks were set at 7% and 15%. We varied the ancestor and which task was riskier.

Figures 2.7 and 2.8 depict the results of the experimental treatments where both tasks are associated with some level of risk. Figure 2.7 depicts the treatments in which task NOT is the riskier task with a 15% lethality risk compared to task NAND with a 7% lethality risk. 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, $p < 0.05$). For example, for the NOT-NAND ancestor, NOT is performed at the mean age of 709.42 ± 9.83 cycles and NAND is performed at the mean age of 469.37 ± 34.42 cycles. For the NAND-NOT ancestor, NOT is performed at the mean age of 591.85 ± 11.29 cycles and NAND is performed at the mean age of 403.56 ± 17.92 cycles. The treatment seeded with the NOT-NAND ancestor reversed the order in which the tasks were performed in 22 out of 30 replicates. Additionally, 30 out of 30 replicates seeded with the NAND-NOT ancestor performed the riskier task NOT at a later age than task NAND.

Figure 2.8 depicts the treatments in which task NAND is the riskier task with a 15% lethality risk compared to task NOT with a 7% lethality risk. In both treatments that vary

the ancestor organism, the mean age at which NAND is performed is significantly greater than the mean age at which NOT is performed (Mann-Whitney U Test, $p < 0.05$). For example, for the NOT-NAND ancestor, NAND is performed at the mean age of 502.83 ± 18.40 cycles and NOT is performed at the mean age of 424.73 ± 27.22 cycles. For the NAND-NOT ancestor, NAND is performed at the mean age of 674.91 ± 21.74 cycles and NOT is performed at the mean age of 445.00 ± 34.38 cycles. 29 out of 30 replicates seeded with the NOT-NAND ancestor performed the riskier task NAND at a later age than task NOT. The treatment seeded with the NAND-NOT ancestor reversed the order in which the tasks were performed in 23 out of 30 replicates.

Figure 2.9 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 three different risk levels associated with tasks. The focus of this section is seen in green with the lethality risks of 7% and 15%. Figure 2.9(a) shows treatments in which NOT has the higher lethality risk. Figure 2.9(b) shows treatments in which NAND is riskier than NOT. We observe that when both tasks are risky, there is a higher selective pressure for completing the riskier task later in life, despite an ancestral genome ordering such that the riskier task was done first. These treatments support our hypothesis that task riskiness can result in temporal polyethism. We observe that the magnitude of risk differential between tasks does not need to be as high if both tasks have some level of risk associated with them.

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

2.4 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 2.10 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.

2.5 Genomic analysis case study

Next, we examined the behavior of a successful group from our two-task experiment 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 2.10). The organisms within this group executed a precise behavioral plan that is depicted in the phenotype portion of Figure 2.11. 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.

A second topic we explored was how the genome architecture of this case study supported this behavior. For example, organisms may have rearranged their genome to support task ordering (i.e., by moving the 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 2.11, 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 2.11 depict the order in which the elements of the genome were executed.

2.6 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 risks associated with performing tasks are removed from the system.

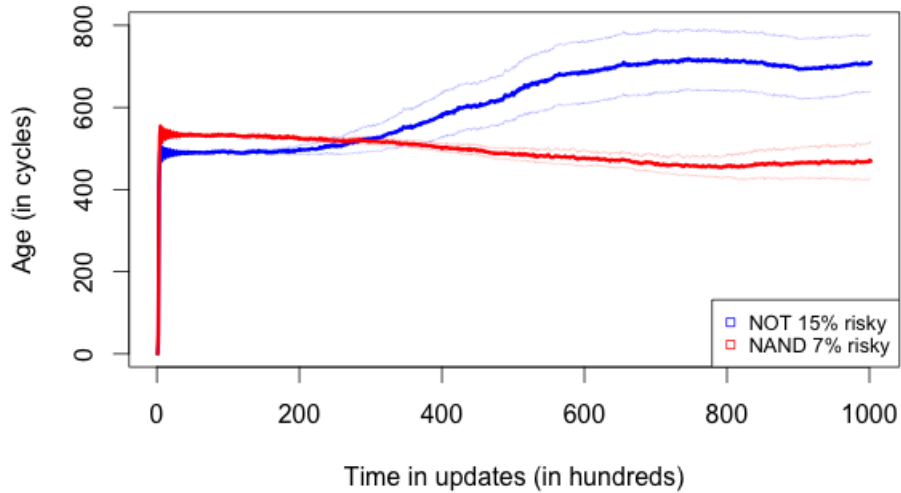
For this analysis, we used the case study whose genotype and phenotype are depicted in Figure 2.11. The results of the three measurements are shown in Table 2.2. All three measurements provide similar results for the age of the non-risky task (NAND). The results vary for the risky task. Specifically, the mean first age for task NOT (964 cycles) is substantially less than the mean age (1103.78 cycles), which in turn is substantially less than the mean age without lethality (1515.02 cycles). 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.

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

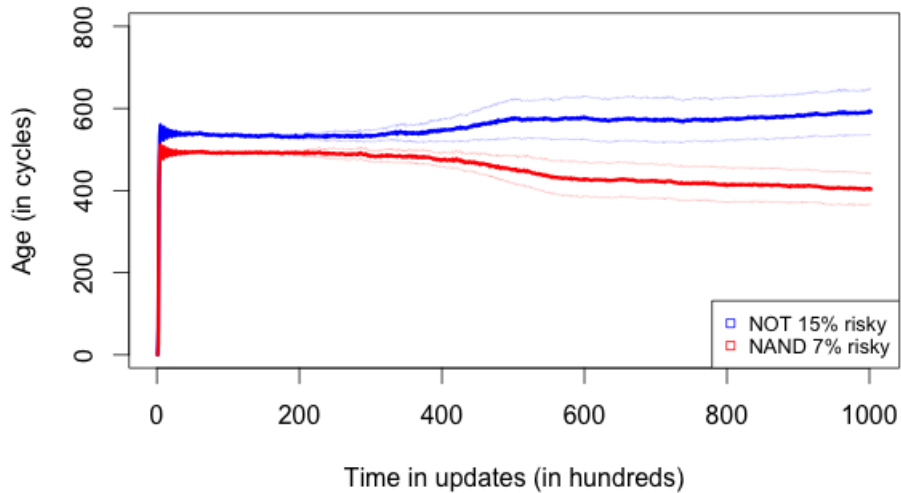
Table 2.2: Three different measurements of the age (in cycles) at which organisms perform a task. While all three have similar results for the non-risky task (NAND), the results differ a bit more for the risky task (NOT). However, all three measurements report a highly significant and substantial difference in mean ages between the two tasks and thus capture the temporal polyethism structure.

2.7 Conclusion

In this chapter, 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 assigning different lethality risks to various types of tasks was a sufficient pressure to produce a temporal polyethism, where organisms performed the least risky task earlier in their lifetime and then switched 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.

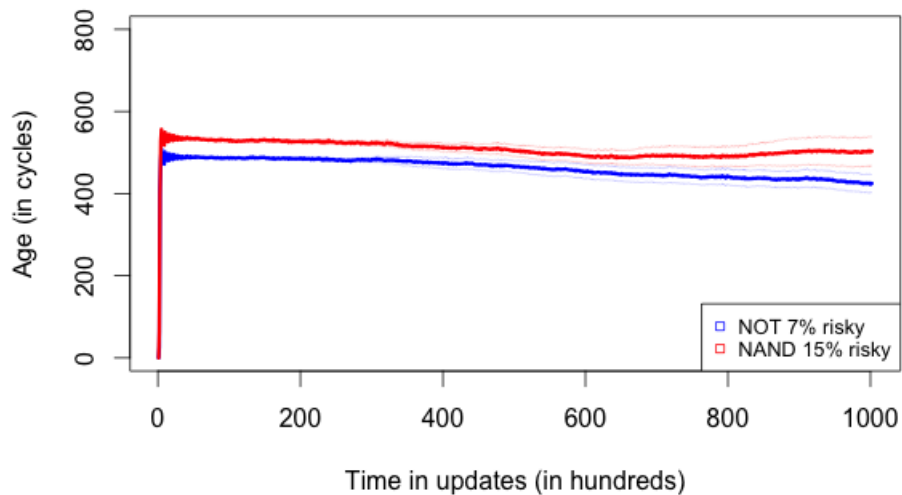


(a) Ancestor: NOT-NAND; Treatment: NOT 15% and NAND 7%

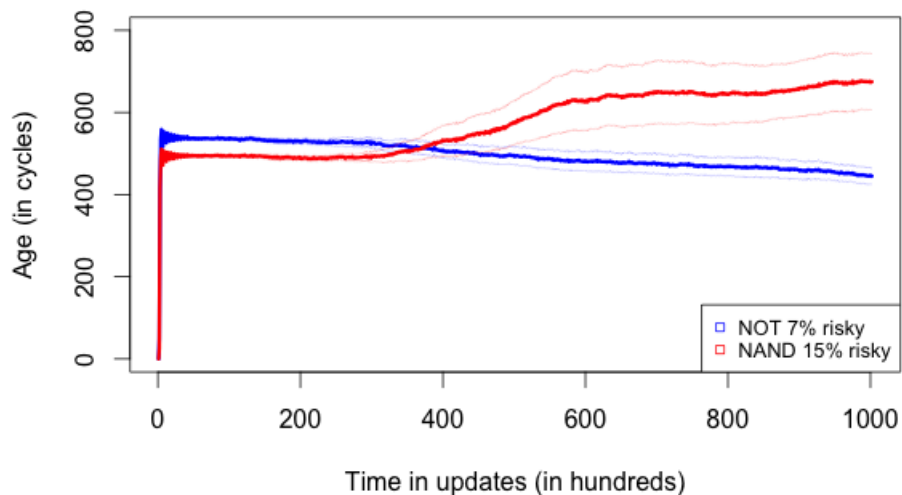


(b) Ancestor: NAND-NOT; Treatment: NOT 15% and NAND 7%

Figure 2.7: 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. Thin lines represent standard error. Task NOT is consistently performed later in the lifetime of the organisms, no matter the starting order.

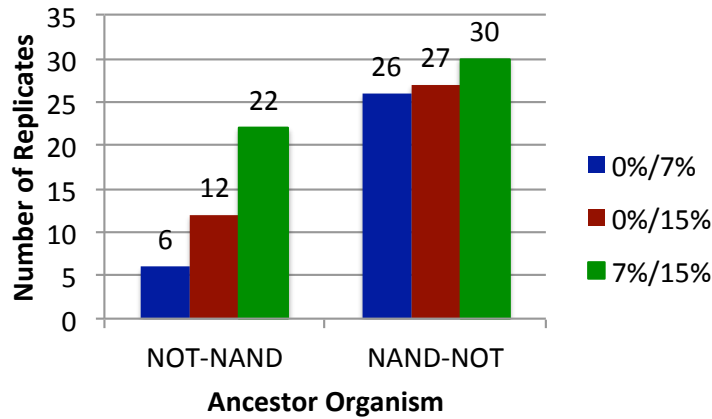


(a) Ancestor: NOT-NAND; Treatment: NOT 7% and NAND 15%

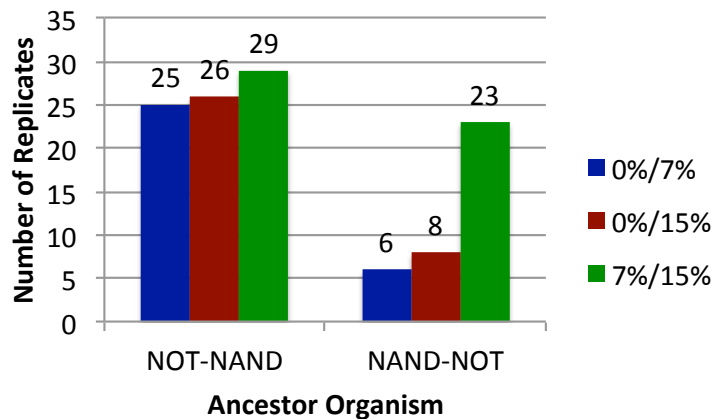


(b) Ancestor: NAND-NOT; Treatment: NOT 7% and NAND 15%

Figure 2.8: Task ordering over time in treatments where task NOT has a 7% lethality risk and task NAND has a 15% lethality risk 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, no matter the starting order.



(a) Treatment: NOT is risky



(b) Treatment: NAND is risky

Figure 2.9: The results of the temporal polyethism treatments, where risk level was varied such that both tasks had some level of risk—7% and 15% are shown as well as two comparison risk levels (0%/7% and 0%/15%). 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 15% risky task and NAND is the 7% risky task. (b) shows results from when NAND is the 15% risky task and NOT is the 7% risky task. The key denotes the lethality risks for the two tasks. Selection for a temporal polyethism pattern is higher when both tasks are risky.

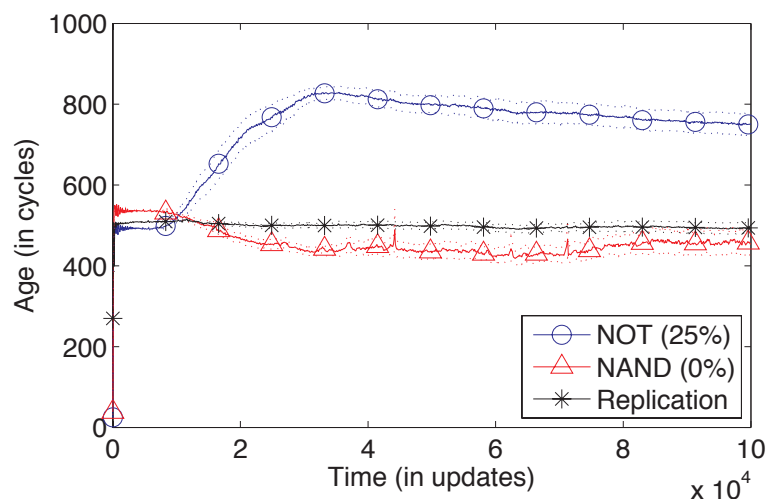


Figure 2.10: These results depict the mean age at which task NOT (blue line with circles), task NAND (red line with triangles) and replication (black line with stars) are performed for the case study treatment where NOT is risky and the runs were started with the NOT-NAND ancestor. These results suggest that the organisms are performing task NAND one or more times, replicating, and then performing task NOT.

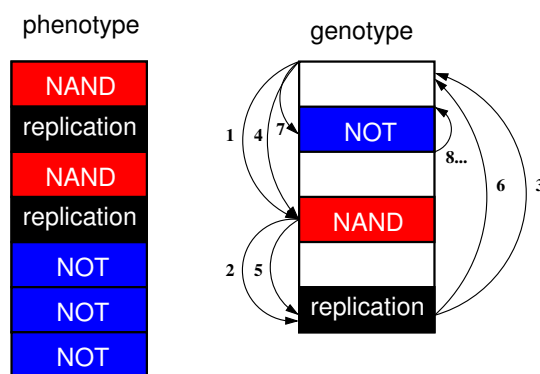


Figure 2.11: Diagrams of the phenotype (left) and genotype (right) of a case study organism whose group exhibited temporal polyethism with two tasks. The numbered arrows surrounding the genotype indicate the order in which instructions were executed to produce the phenotype. In this case, the genotype 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.

Chapter 3

TEMPORAL POLYETHISM WITH THREE TASKS

In the previous chapter, we observed the evolution of temporal polyethism in an environment in that groups performed two tasks. In this chapter, we examine a more complex case where colonies are required to perform three tasks to see if additional tasks lead to more complex forms of temporal polyethism.

3.1 Experimental design

In the three-task environment, colonies must perform tasks NOT, NAND, and ORNOT 250 times each in order for the colony to replicate. We started with three risk levels associated with the tasks – 0% lethality, 7% lethality, and 15% lethality. Using these risk levels, we created eight treatments (described in Table 3.1) to explore all possible matchings between tasks and riskiness levels. The last two treatments (0-0-0 and 7-7-7) are controls in which either none of or all of the tasks are risky. A 15-15-15 control treatment is not possible as all populations die out due to the high lethality levels.

Task	Risk Treatments							
	0-7-15	0-15-7	7-0-15	7-15-0	15-0-7	15-7-0	0-0-0	7-7-7
ORNOT	0%	0%	7%	7%	15%	15%	0%	7%
NOT	7%	15%	0%	15%	0%	7%	0%	7%
NAND	15%	7%	15%	0%	7%	0%	0%	7%

Table 3.1: The eight risk treatments for a three-task environment. The rows describe the lethality risks associated with tasks NOT, NAND, and ORNOT. The columns describe the lethality risks associated with a specific treatment.

Additionally, we created six ancestor organisms (depicted in Figure 3.1) that represent all possible orderings for performing each task once, followed by self-replication. However, each

ancestor organism performs the three tasks in a different order. These ancestor organisms seeded the initial colonies. Again, 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 a total of 30 replicates in each of the eight treatments (described in Table 3.1) that vary the risk associated with the three tasks for a grand total of 1,440 trials. Our hypothesis for these experiments remains the same: task riskiness is a sufficient pressure to result in temporal polyethism regardless of which of the tasks is more risky or the ancestor organism. However, we expect it should be more challenging for colonies to evolve temporal polyethism in this environment because the differences between the risk levels of the tasks is smaller and thus selection may be weaker as evidenced by the two-task results in Figure 2.6.

3.2 *Three-task trial results*

Figures 3.3-3.5 depict the results of the treatments for the ORNOT-NOT-NAND ancestor. The results from the other experiments that use different ancestors were qualitatively similar and thus, the results are not displayed. We calculated the ordering of tasks in two different ways. In the first way, depicted in Figure 3.2, we show the permutation of tasks based on how they reordered tasks based on lethality. In this calculation, we look at the final ordering of tasks based on the average age of task completion in the final population. For example, the expected reordering of tasks under our hypothesis would be 123, wherein 1 indicates that the least risky task was done earlier in life and the 3 indicates that the most risky task was done later in life. In Figure 3.3, we see that runs seeded with particular risk orderings for the ancestral organism (0-7-15, 7-15-0, 15-7-0) do better than others (0-15-7, 7-0-15, 15-0-7). However, in each case, at least two-thirds of the replicates were able to rearrange their genome so that the most risky task (3) with a 15% lethality was done last. This result is not surprising as demonstrated earlier in Figure 2.6, where we see that there is not strong of a evolutionary pressure to rearrange task ordering when lethality risks are associated with the first two tasks are 0% and 7%. As seen in Figure 2.9, there is high enough selection to perform a task with 15% lethality after a task with 7% lethality, consistent with our results that show that the task with the highest magnitude of risk was performed later in

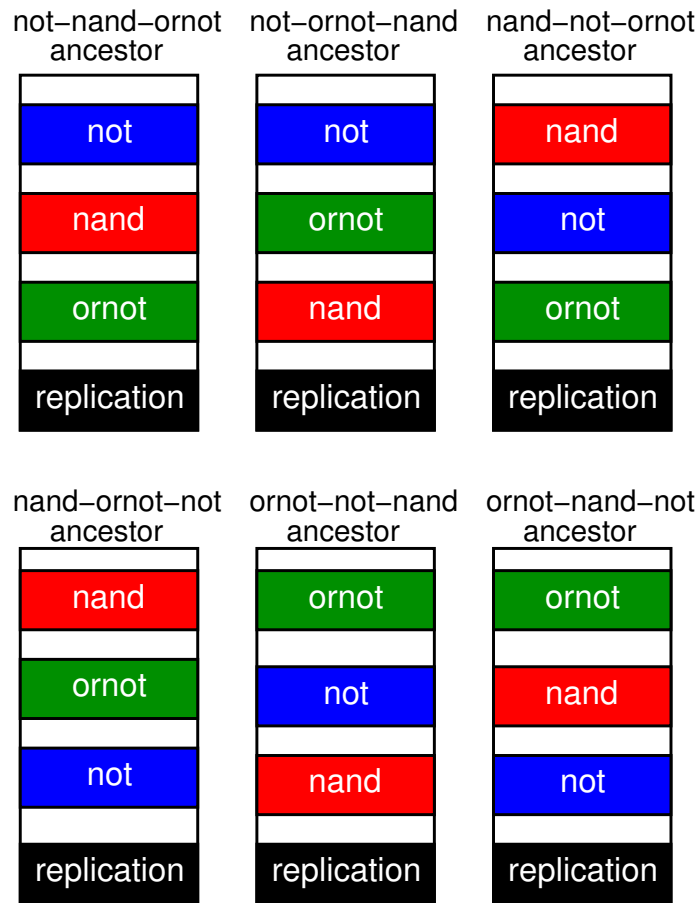


Figure 3.1: The six ancestor organisms for the three-task temporal polyethism experiments. These ancestor organisms vary the order in which the three tasks are performed. Because the genomes are circular, after each organism replicates, it resumes execution at the top of its genome.

life compared to the two other tasks with lower risk levels.

The second way that we calculated the ordering of tasks was to look at how the tasks were reordered compared to the ancestor organism. This metric allows us to look at the permutations of the organisms in the control environments as well. In this calculation, the starting organism's genome orders the tasks as such: ABC. We look at the end ordering of tasks by average age of task completion. In Figure 3.4, we explain the possible task rearrangement permutations. For example, if the starting organism had the genome ORNOT-NOT-NAND, a replicate with the end permutation of BCA would have the NOT done earlier in

life, followed by NAND, and lastly, ORNOT. We would expect that if the ancestral organism did not convey any bias, we would see equal probabilities for the task permutations of the end populations. Figure 3.5 depicts our results. First, we see that 3 permutations (ABC, ACB, BCA) encapsulate almost two-thirds of all permutations in each environment including the controls. Second, we see that in the control environment, where the three tasks have a 7% lethality risk associated with them, 28 out of 30 replicates stay in the ancestral permutation of ABC; whereas, the control with 0% lethality across each task were able to evolve to rearrange their genomes more readily. Equal probabilities for each permutation was expected for both control environments; however, this is not the case in the 7-7-7 treatment (Fisher's exact test, $p < 0.05$). Together, these results indicate that there is a bias that affects the ability to change the permutation of tasks.

3.2.1 Next Steps

To attempt to identify the source of this bias and correct it in future experiments, the following experiments were performed:

1. Are some tasks inherently more complex than others?
2. Do small group sizes limit evolutionary potential?
3. Does the number of tasks needed for colony replication alter division-of-labor patterns?
4. Will varying risk levels increase evolutionary pressure for temporal polyethism to emerge?
5. Can combining these pressures increase the pressure for evolution of temporal polyethism?

3.3 Task complexity changes

To address the bias, we first examined the tasks themselves to see if there was any inherent bias associated with them. The task ORNOT is more computationally complex than the tasks NOT and NAND. To address this, we chose ADD, which is computationally similar to NAND. We ran the same setup as earlier with the 8 different environments as seen in Table 3.1. In Figure 3.6, we see a similar pattern to the earlier treatments with ORNOT, with the corresponding ancestor organism of ADD-NOT-NAND. Therefore, we believe that the task complexity was not the source of the bias.

3.4 *Population size changes*

Next, we changed the sizes of the colonies themselves. Our hypothesis was that it may be difficult for organisms to complete tasks, replicate, and rearrange their genome when there were so few individuals. We changed the colony size in two ways - we went from the original 25 organisms in each of 400 colonies to 50 organisms in each of 200 colonies as well as 250 organisms in each of 40 colonies while maintaining the overall population size of 10,000. In the experiments where it was possible to have 250 organisms in each colony, we believed that there would not be enough pressure to rearrange tasks to avoid dying as each organism only had to complete each task once or twice to fulfill their obligation to the colony as a whole. The biological analog would be that each member of a bee colony would unrealistically have to do each task only once before replicating. This experiment was done as a control to see the effect of large colony sizes.

In Figures 3.7 and 3.8, we see that there are qualitatively similar results for the most popular permutations. While we do see an increase in the number of replicates that are able to rearrange to permutation ACB, CAB, and CBA when there are 200 colonies of 50 organisms, the result is not significant (Fisher's exact test, $p > 0.05$). However, we believe that there may be an optimal colony size between 25 organisms and 250 organisms. As colony size increased, the pattern of task permutations changed significantly in the 0-0-0 and 7-7-7 control treatments (Fisher's exact test, $p < 0.05$). As colony size increased, there was more evolution towards different task permutation patterns in the 7-7-7 control treatment. Oppositely, there was more of a selective pressure to keep the ancestral task ordering when colony size increased in the 0-0-0 control treatment. In a biological sense, it is possible that colonies of different sizes can have different division of labor techniques to mediate between colony size and need to complete tasks. If the colony is large such that each organism only has to complete each task once or twice in its lifetime, there is not as much of a pressure to optimize how the colony members perform tasks. Conversely, if the colonies are smaller and each member has to perform tasks with lethality risks multiple times, there is a pressure to conserve the workforce. The size of the colony could explain some of the bias as the total number of organisms in a colony is computationally limited,

but more work needs to be done in this area.

3.5 Changes to the number of tasks required for colony replication

The next thing we tried was to see if changing the number of tasks required for colony replication could affect the evolution of temporal polyethism. We raised the number of tasks that colonies had to complete in order to replicate to 500 tasks of each type. Our hypothesis was that by increasing the number of tasks that the colony had to do, we would increase the pressure to keep the colony members alive to complete tasks, and therefore, there would be a higher pressure to do riskier tasks later in life. Contrarily, in Figure 3.9, we see a significant decrease in the number of runs that are able to evolve a temporal-polyethism pattern in two treatments: 0-15-7 and 15-0-7, but no significant change in the other treatments (Fisher's exact test). We see that most of the experiments ended with the same ordering of tasks as the ancestral organism.

We thus examined what would occur when we lowered the number of tasks needed for colony replication. Our hypothesis was that if we lowered the tasks needed for colony replication, there would be less pressure for the colony as a whole to complete tasks, and there could be more room for exploring evolutionary space by rearranging genomes. In this case, there is more colony replication, and therefore, more generations of colonies. In Figure 3.10, there is a significant increase in the number of replicates that are able to evolve the permutation CAB when it is the permutation that has the riskiest task done last, supporting the temporal-polyethism pattern (Fisher's exact test, $p < 0.05$). The 0-0-0 control treatment also had a significant increase in the number of replicates that could rearrange their task completion from the ancestral ordering (Fisher's exact test, $p < 0.05$). However, all other treatments are similar between this treatment and the original (Fisher's exact test, $p > 0.05$). Together, these results indicate that there may be a selective effect from lowering the number of tasks needed from colony replication, but more research needs to be completed in this area.

3.6 Varying risk levels

As mentioned earlier, the selective pressures to rearrange tasks were weaker when there is lower variance in risk levels between tasks. To remedy this, we tried a variety of different risk levels.

3.6.1 0%, 10%, 20%

We tried a small increase in the risks associated with tasks by changing the three levels to 0%, 10%, and 20%. In Figure 3.11, we see the results of all 8 environments with the ancestral organism of ADD-NOT-NAND have similar results. This result was expected as there is not a high selective pressure to evolve to reorder the least risky task of 0%.

3.6.2 0%, 18%, 28%

We tried another increase in the risks associated with tasks by changing the three levels to 0%, 18%, and 28%. This increase proved to be too high in terms of lethality as the colonies stopped replicating after approximately 4000 updates. We tried to lower the number of tasks that needed to be completed for colony replication from 250 tasks to 100 tasks; however, there was still a stop to colony replication.

Our next attempt involved increasing the size of the colonies from 25 organisms to 50 organisms so that there would be more organisms that could attempt to complete tasks. Despite this increase in colony size, we observed that colony replication prematurely ended. We believe that this is an artifact of the colony replication itself. When a colony replicates, one organism seeds the new colony. In the beginning stages of the colony, there are few organisms, and they are more susceptible to dying. For example, if a colony starts with an ancestor organism that does the riskiest task first, 28% of all colonies die before the ancestor can replicate to increase colony size to two organisms. The biological equivalent would be one bee starting a new colony and dying while foraging before the colony could increase in size. To address this concern, we tried to increase the size of the propagule from 1 organism to 25 organisms so that the new colonies are starting out completely full (the colony size was decreased again to 25 organisms). This change, however, removed pressures

to do riskier tasks later in life as each colony started at full capacity, and we do not observe a temporal-polyethism pattern where the riskiest task is done later in life.

3.6.3 0%, 18%, 18%

As we see that in the two-task trials, lethality risks higher than 15% lead to dramatically higher numbers of replicates that are able to rearrange their ancestral genome to have the riskier task done later in life. As our earlier trials with higher risks resulted in loss of colony replication, we tried lowering the lethality to a total of 36%, by having one 0% task and two 18% tasks. We see again that, again, colony replication stops for most replicates.

3.6.4 *Combination of pressures*

We combined a variety of the previously mentioned pressures: lethality risks associated with tasks were increased to 0%/10%/20%, there were 50 organisms in each of 200 colonies, and the task requirement was lowered to 150 tasks each for colony replication. Each of these changes increased the overall number of generations for each replicate. In Figure 3.12, we see that the combination of pressures leads to the evolution of the less popular permutations of BAC, CAB, and CBA. In fact, there was a significant increase in the evolution of different task permutations in all of the treatments except for 0-7-15 where the ancestor already had a temporal polyethism pattern and in the 0-0-0 control (Fisher's exact test, $p < 0.05$). We observe that the control with a lethality risk of 7% across each of the tasks had a substantial increase of replicates that were able to evolve to do the three tasks at different points in their life as compared to the ancestor (Fisher's exact test, $p < 0.05$). These results indicate that there are a variety of selective pressures that work together towards the evolution of temporal polyethism.

3.7 *Discussion*

In this chapter, we examined the evolution of temporal polyethism with more complex colonies that need to complete a certain number of three tasks for colony replication. We found that there was a bias that prevented the trivial rearrangement tasks in organisms'

genomes. To address this constraint, a variety of experiments were performed: task complexity shifts, increases to the number of organisms in a colony, changes to the number of tasks needed for colony replication, and variation in the lethality risk levels associated with tasks. We observed that the size of colonies affects the evolution of division-of-labor strategies. However, having an increased number of colony generations through lowering the threshold for colony replication does, in selected instances, increase the likelihood for the evolution of division of labor. Increasing the lethality risks associated with tasks did not significantly change the pressures for the evolution of temporal polyethism. This was expected as we saw in Chapter 2 that there is little pressure to rearrange the least risky task as there is no lethality associated with it. Our bias was remedied when we combined a variety of selective pressures - fewer tasks for colony replication, higher lethality risks associated with tasks, and larger colony sizes. In Table 3.2, we summarize the data, and we see that almost all treatments had at least two-thirds of all replicates evolved to rearrange their genome so that the riskiest task was done last in life.

Treatments	Original	Task Complexity - ADD	50 Organisms / Colony	250 Organisms / Colony	500 Tasks / Colony Replication	150 Tasks / Colony Replication	0%/10%/20% Lethality Risks	Combined
0-7-15	83%	87%	83%	83%	90%	80%	83%	67%
0-15-7	83%	67%	80%	60%	60%	87%	77%	53%
7-0-15	83%	73%	93%	77%	90%	77%	70%	83%
7-15-0	77%	83%	90%	77%	50%	80%	73%	73%
15-0-7	80%	87%	77%	70%	70%	97%	83%	70%
15-7-0	70%	80%	90%	70%	60%	90%	90%	63%

Table 3.2: Results from all of the experiments with three tasks. Each percentage represents the number of runs from each treatment where the riskiest task was evolved to be done last in life. We focus on the riskiest task because there was weaker pressure to rearrange the two less risky tasks. We see that in most cases, over two-thirds of the replicates have the temporal-polyethism pattern where the riskiest task was done last. Two cases in particular had over three-fourths of replicates evolve to rearrange their genome so the riskiest task was done last – the treatment with 50 organisms per colony and the treatment where only 150 tasks instead of 250 tasks were needed for colony replication.

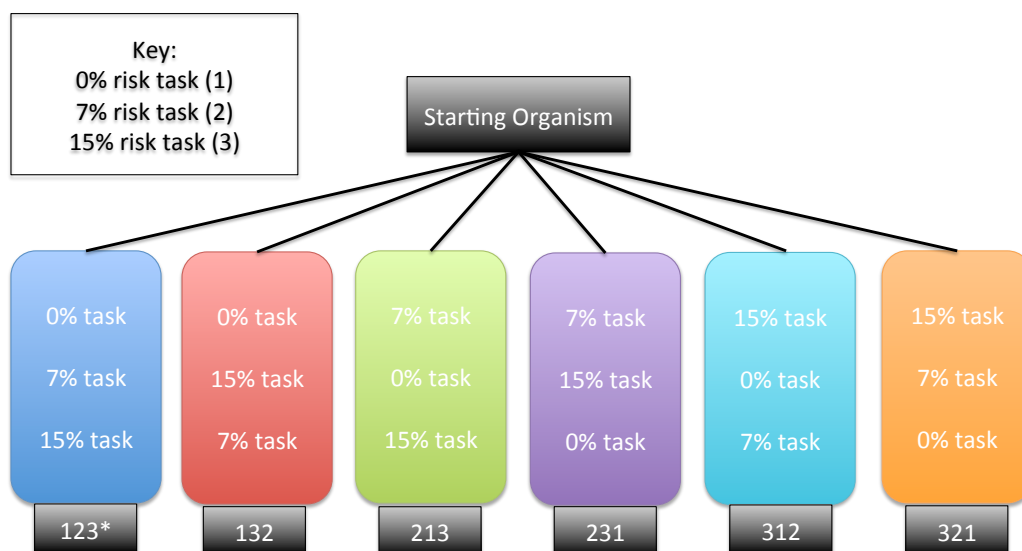


Figure 3.2: We start with one ancestor organism and then analyze the resulting average ages of task completion to assess whether evolution favored organisms that do tasks at different points in their lives based on lethality risks. The six possible task risk permutations at the end of each treatment are shown in the colored boxes. In the black boxes at the bottom, 1 corresponds to the least risky task with 0% lethality, 2 corresponds to the middle task with 7% lethality, and 3 corresponds to the most risky task with 15% lethality. If the temporal polyethism hypothesis holds true, we expect to see end populations have task ordering of 123, in that they do the least risky task earlier in life and the most risky task later in life. The combination of the three numbers indicate the task ordering by average age of task performance in the population at the end of the run.

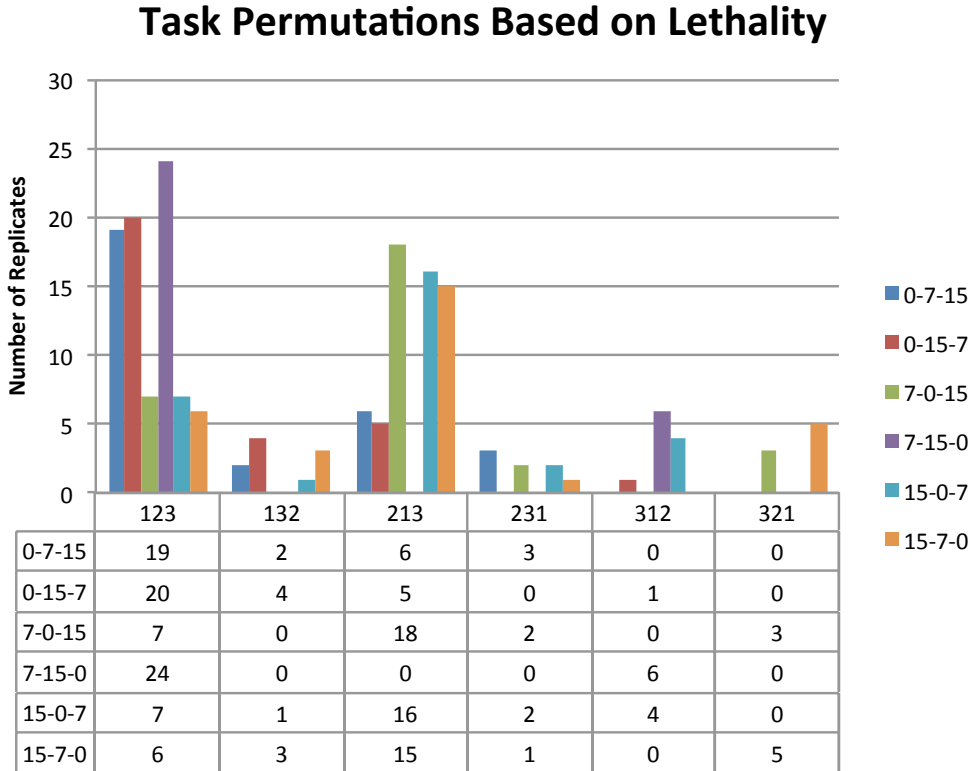


Figure 3.3: Count of final task orderings across environments except the controls. The runs were seeded with ancestor organism ORNOT-NOT-NAND and run in all eight environments noted in Table 3.1. There are six possible task risk permutations. 1 corresponds to the least risky task with 0% lethality, 2 corresponds to the middle task with 7% lethality, and 3 corresponds to the most risky task with 15% lethality. If the task-riskiness hypothesis holds true, we expect to see end populations have task ordering of 123, in that they do the least risky task earlier in life and the most risky task later in life. We expected to see the majority of the replicates to fall under the 123 category, but what we see is that the highest number of replicates is spread out between 123 and 213, indicating that the organisms were able to at least complete the most risky task last in life.

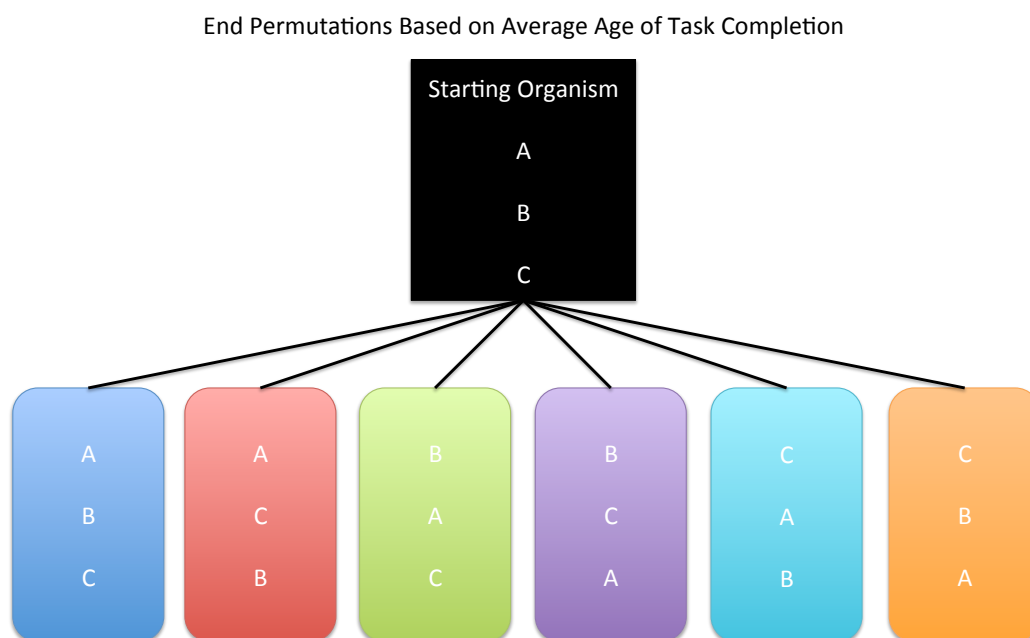


Figure 3.4: The ancestor organism is shown in the black box, and the ordering of tasks in the genome is denoted by ABC with A being the task earliest in the genome, B being the middle task, and C being the last task. Below in the colored boxes, permutations of the task ordering for the three-task temporal polyethism experiments is shown as compared to the ancestral organism. For example, the ancestor organism ORNOT-NOT-NAND would have the letter A corresponds to the first task of ORNOT, B corresponds to NOT, and C corresponds to NAND. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run. We expect that if each task has equal lethalties as in our controls, we would see equal probabilities for all six of the end permutations.

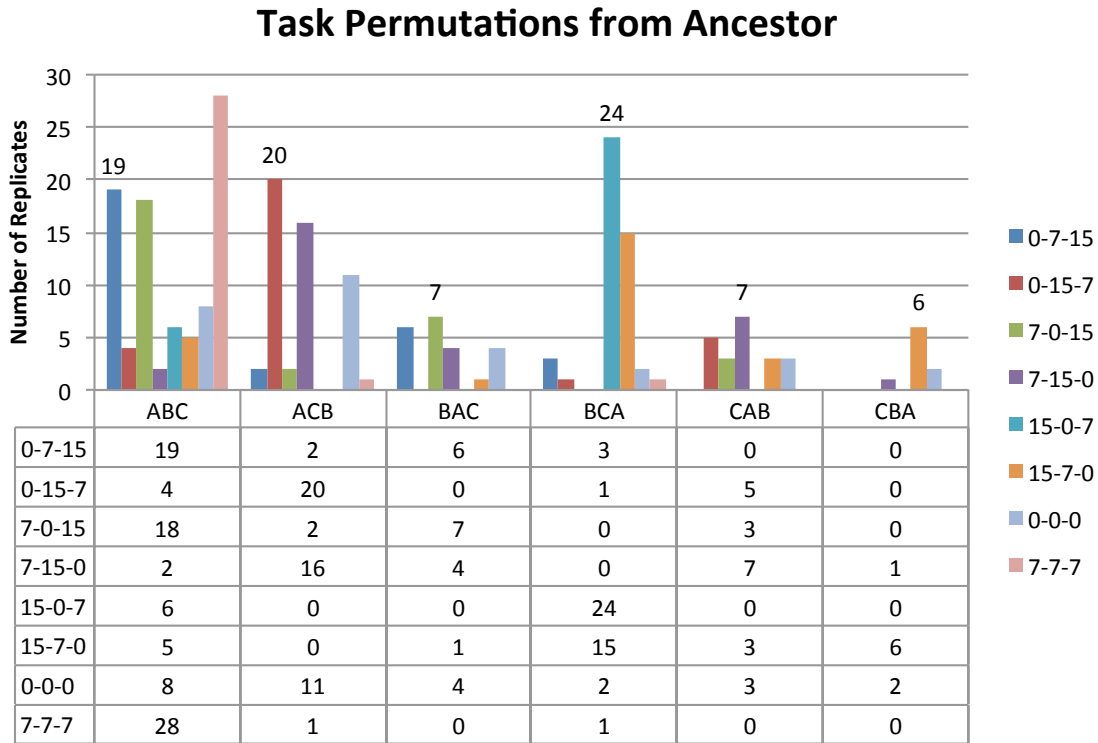


Figure 3.5: A graph of the permutations of the task ordering from runs were seeded with ancestor organism ORNOT-NOT-NAND, run in all eight environments noted in Table 3.1. The data shown is the task rearrangement from the original ancestor organism of ORNOT-NOT-NAND, denoted as ABC. The letter A corresponds to the first task in the starting organism's genome, ORNOT, B corresponds to NOT, and C corresponds to NAND as seen in Figure 3.4. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run. Bars with numbers above them indicate the permutation that would be expected under the task-riskiness hypothesis. We see that three permutations (ABC, ACB and BCA) encapsulate more than two-thirds of the final task permutations indicating that there is a bias affecting the rearrangement of tasks. We expect to see equal probabilities for all 6 permutations for both of our control treatments, however, this is not the case (Fisher's Exact Test).

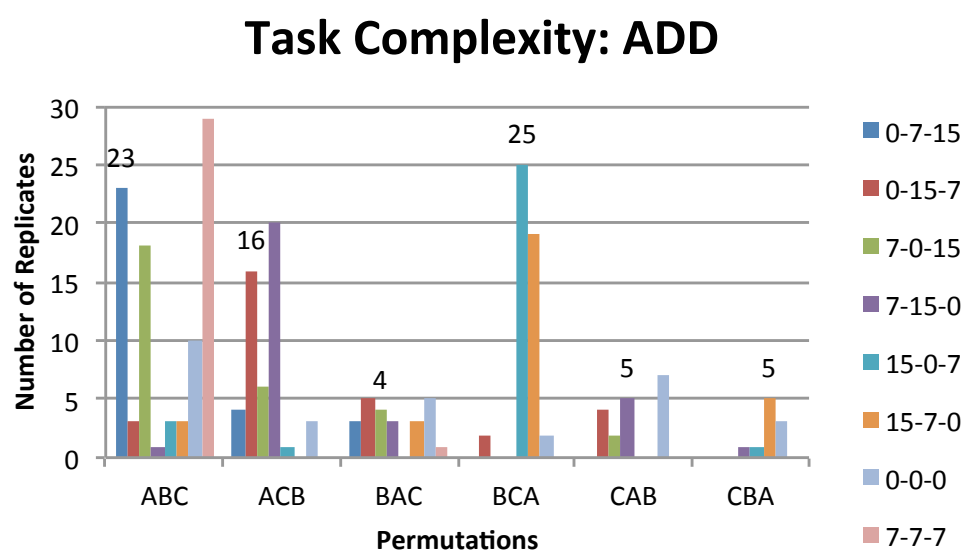


Figure 3.6: A graph of the permutations of the mean age of task for the final population from runs where the task complexity was changed from ORNOT to ADD. The data shown is the task rearrangement from the original ancestor organism of ADD-NOT-NAND, denoted as ABC. The combination of the three letters indicates the task ordering by average age of task performance in the population at the end of the run as seen in Figure 3.4. Bars with numbers above them indicate the permutation that would be expected under the task-riskiness hypothesis. We see a similar pattern in task permutations with task ADD as when we had task ORNOT in the genome.

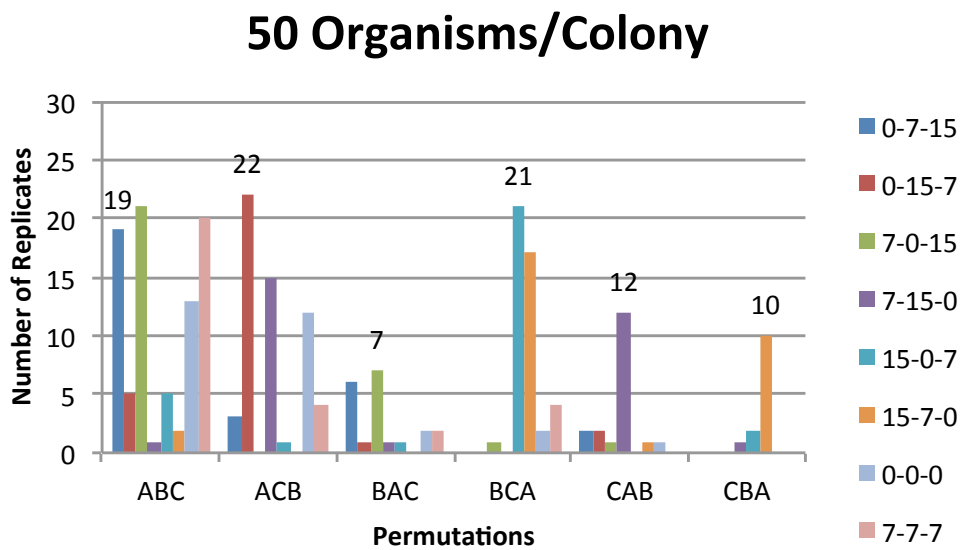


Figure 3.7: A graph of the permutations of the mean age of task for the final population where there were 50 organisms in 200 colonies. The data shown is the task rearrangement from the original ancestor organism of ADD-NOT-NAND, denoted as ABC. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run as seen in Figure 3.4. Bars with numbers above them indicate the permutation that would be expected under the task-riskiness hypothesis. We see that there is a significant change in the number of replicates that can rearrange their genome for the control treatments of 0-0-0 and 7-7-7 (Fisher's exact test, $p < 0.05$).

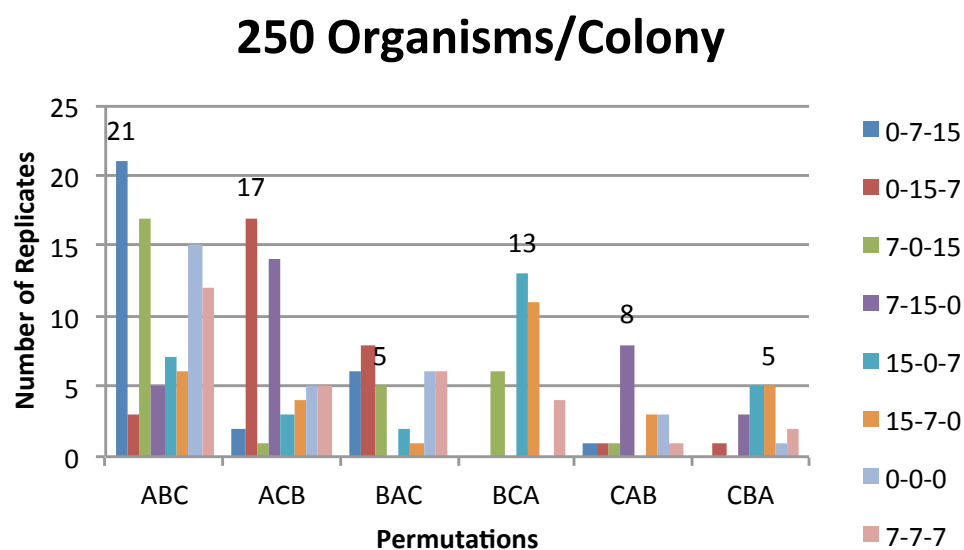


Figure 3.8: A graph of the permutations of the mean age of task for the final population with 250 organisms each in 40 colonies. The data shown is the task rearrangement from the original ancestor organism of ADD-NOT-NAND, denoted as ABC. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run as seen in Figure 3.4. Bars with numbers above them indicate the permutation that would be expected under the task-riskiness hypothesis. We see that the results from having 250 organisms in one colony are qualitatively similar to when there are 25 organisms in one colony. We also see that there is a significant change in the number of replicates that can rearrange their genome for the control treatments of 0-0-0 and 7-7-7 (Fisher's exact test, $p < 0.05$).

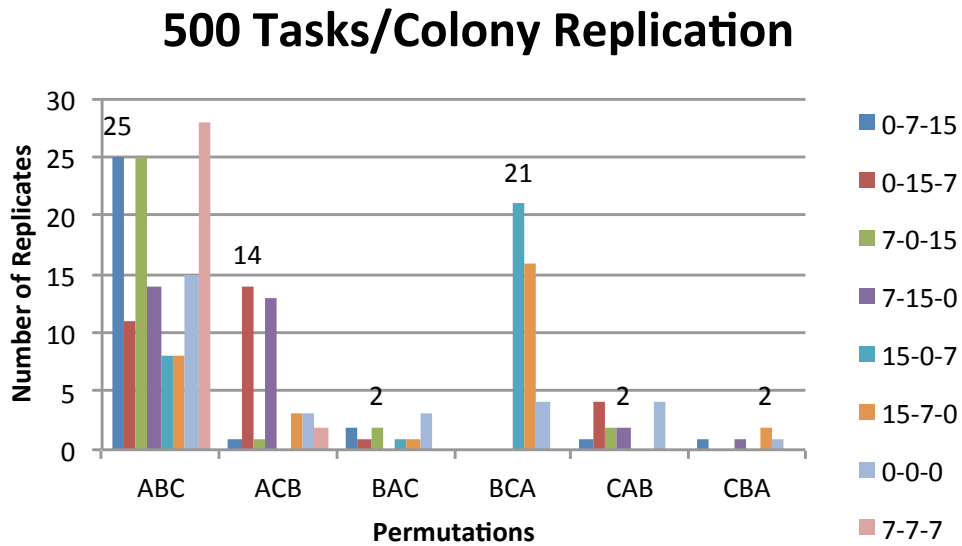


Figure 3.9: A graph of the permutations of the mean age of task for the final population in runs where 500 tasks were needed for colony replication. The data shown is the task rearrangement from the original ancestor organism of ADD-NOT-NAND, denoted as ABC. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run as seen in Figure 3.4. Bars with numbers above them indicate the permutation that would be expected under the task-riskiness hypothesis. We see a significant decrease in the number of runs that are able to evolve a temporal-polyethism pattern in two treatments: 0-15-7 and 15-0-7, but no significant change in the other treatments (Fisher's exact test).

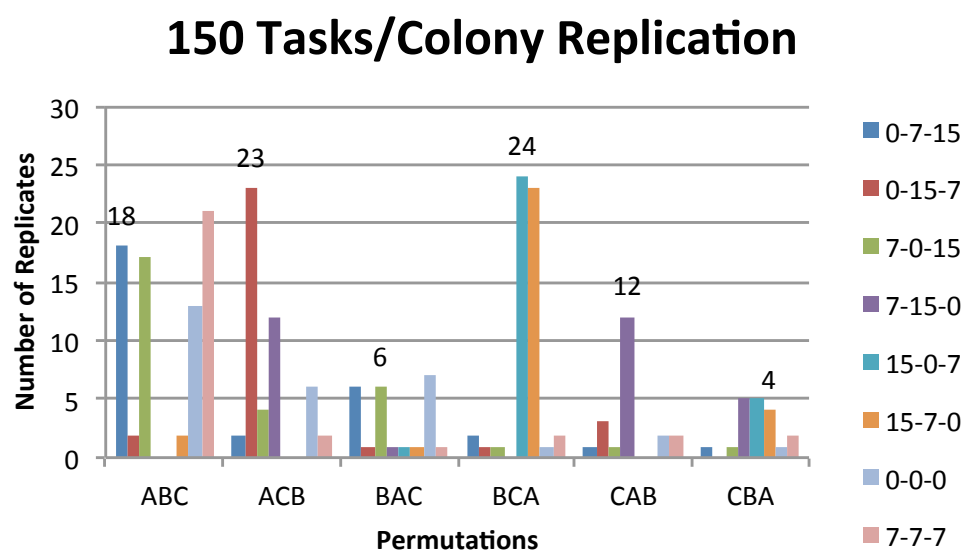


Figure 3.10: A graph of the permutations of the mean age of task for the final population in runs where 150 tasks were needed for colony replication. The data shown is the task rearrangement from the original ancestor organism of ADD-NOT-NAND, denoted as ABC. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run as seen in Figure 3.4. Bars with numbers above them indicate the permutation that would be expected under the task-riskiness hypothesis. We see a significant increase in the number of replicates that are able to rearrange to permutation CAB, but otherwise qualitatively similar results.

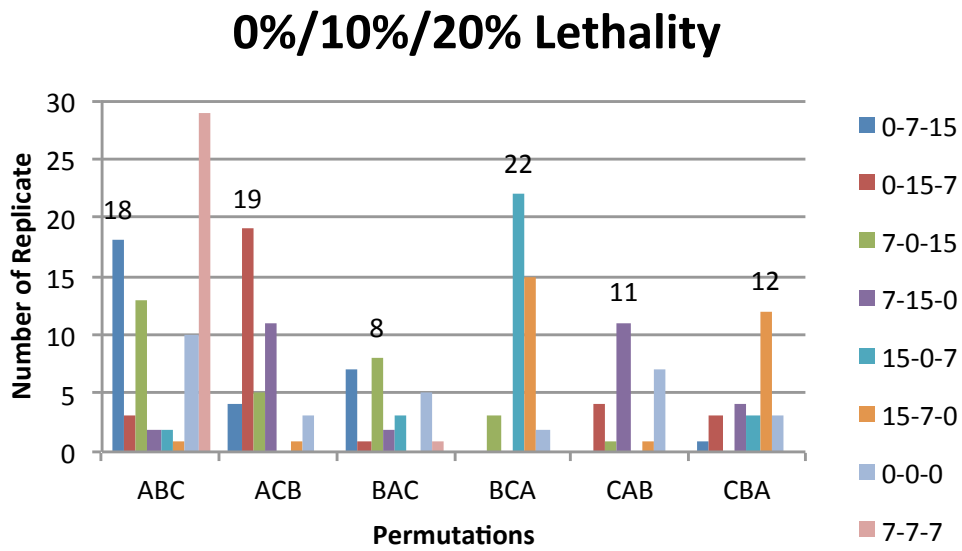


Figure 3.11: A graph of the permutations of the mean age of task for the final population when the lethalties associated with the tasks were 0%, 10%, and 20%. The data shown is the task rearrangement from the original ancestor organism of ADD-NOT-NAND, denoted as ABC. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run as seen in Figure 3.4. Bars with numbers above them indicate the permutation that would be expected under the task-riskiness hypothesis. We see similar results compared to runs with lethalties 0%/7%/15%.

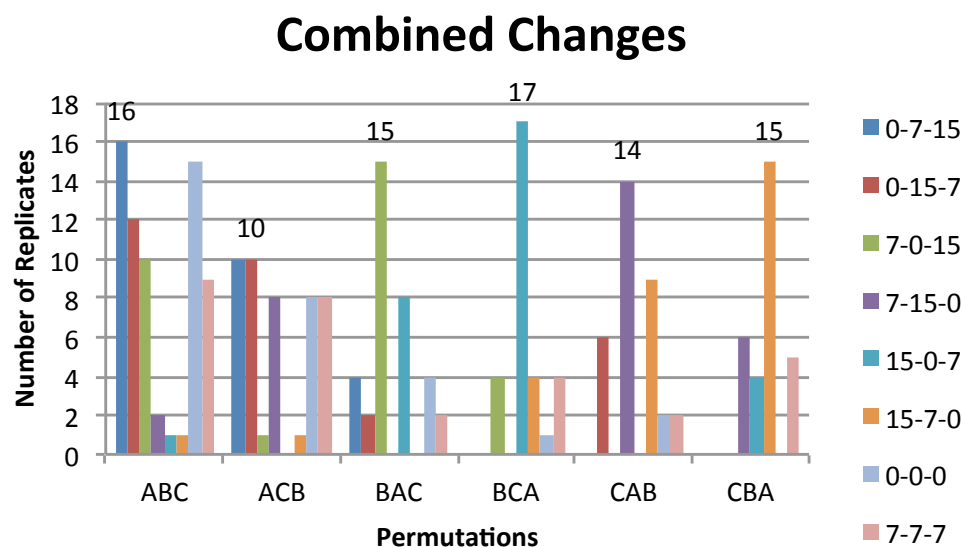


Figure 3.12: A graph of the permutations of the mean age of task for the final population when the lethalties associated with the tasks were 0%, 10%, and 20% in a world with 50 organisms in each of 200 colonies with 150 successful completion of all tasks required for colony replication. The data shown is the task rearrangement from the original ancestor organism of ADD-NOT-NAND, denoted as ABC. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run as seen in Figure 3.4. Bars with numbers above them indicate the permutation that would be expected under the task-riskiness hypothesis. We see that compared to the original runs, there is a significant increase in the number of replicates that have the expected permutation under the task-riskiness hypothesis treatments except 0-7-15 and 0-0-0, indicating that changing multiple pressures increases selection for colonies with a temporal-polyethism pattern.

Chapter 4

TASK-SWITCHING COSTS

In this chapter, we examine the interaction of competing pressures of lethality risks and task-switching costs. The addition of task-switching costs addresses concerns raised about previous models that organisms could freely transition back and forth between tasks without any penalty [22].

4.1 Experimental design*4.1.1 Task-switching costs*

We used the same initial setup at the two- and three-task trials from Chapters 2 and 3. For the two-task trials, the two tasks were NOT and NAND, with risk treatments as noted in Table 2.1. The three tasks trials had the following tasks: NOT, NAND, and ORNOT with the same risk treatments as denoted in Table 3.1. We added a low task-switching penalty of 50 cycles in one set of experiments and a high task-switching penalty of 200 cycles in another set of experiments. In Figure 4.1, we explain the task-switching cost is applied to organisms when they transition between two different tasks. However, there is no penalty when an organism repeats the same task. Thus, an organism who does one task three times followed by another task three times would have to pay the cost only one, while one that toggles back and forth between the tasks would have to pay it five times. We expect this cost to create a pressure to cluster similar tasks, and perhaps to encourage specialization among organisms so that no task-switching costs need be paid at all.

4.1.2 Shannon mutual information

We used the Shannon mutual information to track the degree to which the colonies are exhibiting division of labor [6, 9]. Shannon mutual information gives information about two aspects of division of labor: “(1) given an individual, how much information do we

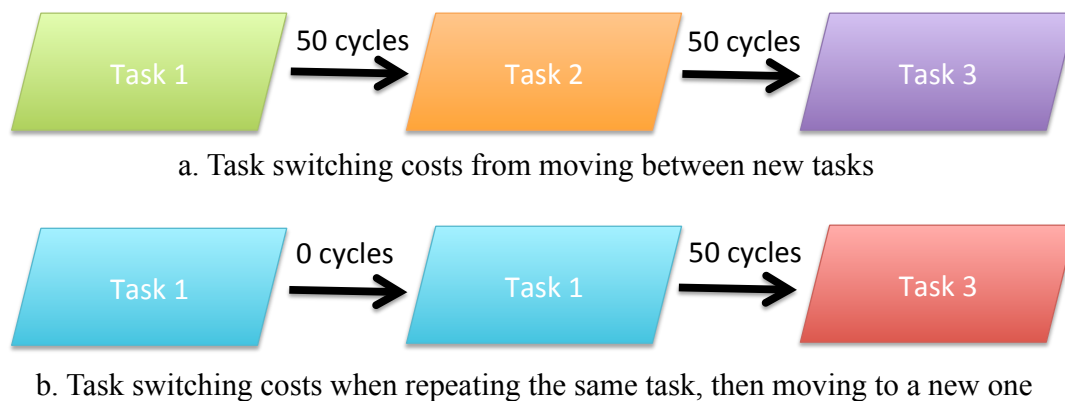


Figure 4.1: This is a diagram of how task-switching costs are applied. Each box represents a task that an organism completes. When an organism transitions from completing one task to attempting another, there is a task-switching penalty of 50 cycles as seen in (a). If an organism repeats the same task, the task-switching cost is avoided as seen in (b).

have about the type task it performs, and (2) given a type of task, how much information do we have about the individual that performed it.” [6]. The higher the Shannon mutual information, the higher the division of labor in colonies. If Shannon mutual information is low, then all individuals in the colony are performing the exact same set of tasks. Shannon mutual information is high when each individual specializes on different tasks, corresponding to high division of labor.

This task-switching cost setup allows us to determine if adding task-switching costs change the mean age at which tasks were performed. This information will help us understand the efficacy of risk in producing a temporal-polyethism phenotype. In addition, we want to see if task-switching costs increase the division of labor within the colony. We expect that task-switching costs would favor specialization over temporal polyethism. Therefore, it will be interesting to determine the interplay between task-switching costs that favor specialization and tasks associated with risks levels that favor temporal polyethism.

4.2 *Two-task results*

4.2.1 *Temporal polyethism*

When we varied the level of task-switching costs, we did not see a difference in the number of replicates that were able to evolve a temporal polyethism pattern. Figure 4.2 shows the number of replicates in each treatment that were able to evolve a temporal polyethism pattern where the riskier task was performed later in life. We see that when there are competing pressures of task-switching costs versus lethality risks associated with tasks, there is still evolution of temporal polyethism, favoring the selective pressure of risk. The number of replicates with the temporal-polyethism pattern across each treatment is similar (Fisher's exact test, $p < 0.05$).

We compared the mean age for both task NOT and NAND at the end of each replicate across the three task-switching cost treatments. In the majority of cases, there was not a substantial difference in mean age of task completion (Mann-Whitney U test, $p > 0.05$). However, when the task-switching cost was high at 200 cycles, there is a significant increase in the mean age of completion of the task NOT in the two treatments where NOT was the risky task with 25% lethality associated with it. When the ancestor organism was NOT-NAND, the increase in mean age was from 654 cycles to 754 cycles. When the ancestor organism was NAND-NOT, the increase was from 687 cycles to 790 cycles. We believe that if the task-switching pressure was raised again, there would be an increase in mean age for other task orderings.

In addition, we found that the mean age of the tasks for the non-lethal controls significantly decreased (Mann-Whitney U test, $p < 0.05$) from the trials with no task-switching costs as compared to both trials with task-switching costs, respectively. For example, when the ancestral organism was NOT-NAND, the mean age for NOT decreased from 721 cycles for no task-switching costs to 543 cycles for low task-switching costs and 525 cycles for high task-switching costs. Similarly, when the ancestral organism was NOT-NAND, the mean age for NAND decreased from 691 cycles for no task-switching costs to 499 cycles for low task-switching costs and 492 cycles for high task-switching.

These results show that when there are no lethality risks associated with tasks, task-

switching costs change the mean ages of task completion. Similarly, when task-switching costs are high, there is potential to increase the mean average age of task-completion, showing that task-switching costs are a competing pressure to lethality risks.

4.2.2 Shannon mutual information

The average final Shannon mutual information value was measured from each replicate. We compared runs of task-switching costs (50 cycles or 200 cycles) with runs that did not have task-switching costs across each treatment. We found that in each case, there was not a statistically significant difference in the Shannon mutual information (Mann-Whitney U test, $p > 0.05$). We believe this result is the case because of the limited number of tasks.

4.3 Three-task results

4.3.1 Temporal polyethism

We see that the addition of task-switching costs does not affect the evolution of temporal polyethism. The task ordering based on average age was not significantly different across task-switching costs levels (Fisher's exact test, $p > 0.05$) for all treatments except the controls. As seen in Figure 4.3 that depicts the controls, we see that when there are no lethality risks associated with all three tasks, task-switching costs affect the evolution of the rearrangement of task orderings such that the majority stay in the ancestral ordering. However, when all of the tasks have a lethality risk of 7%, no ordering on tasks is favored over another as we see in Figure 4.3(b).

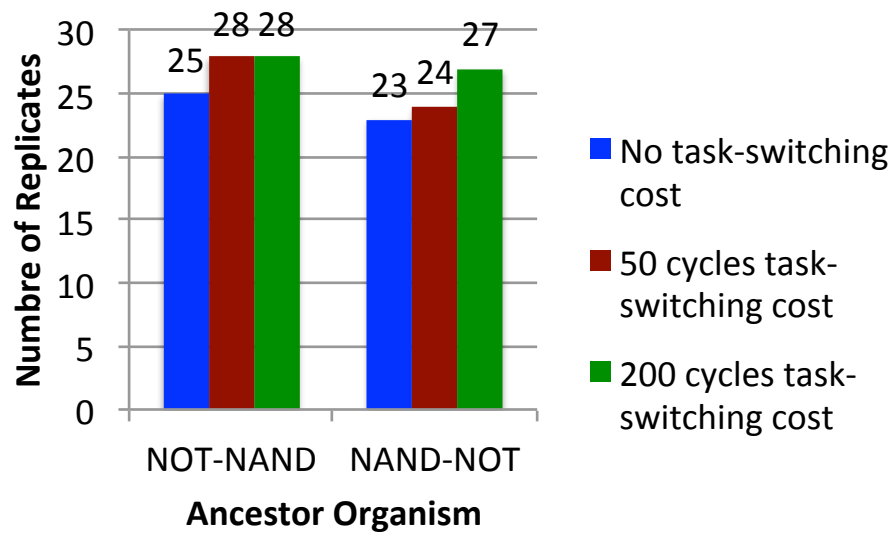
4.3.2 Shannon mutual information

The average final Shannon mutual information value was measured from each replicate. We compared runs of task-switching costs (50 cycles or 200 cycles) with runs that did not have task-switching costs across each treatment. We found that when the task-switching cost was 50 cycles, the control treatments (0-0-0 and 7-7-7) produced significant increases in the average Shannon mutual information at the end of the trials (Mann-Whitney U test, $p < 0.05$). In addition, 2 out of 6 of the other treatments (0-7-15 and 15-7-0) both had significant

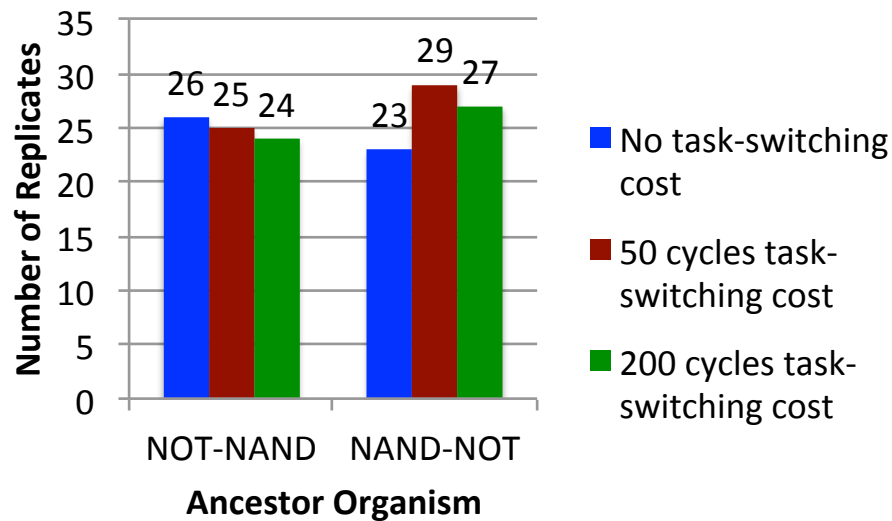
increases in the Shannon mutual information when the penalty was low (Mann-Whitney U test, $p < 0.05$). When the task-switching penalty was increased high at 200 cycles, each risk permutation treatment except for one (0-15-7) had significant increases in Shannon mutual information (Mann-Whitney U test, $p < 0.05$). In Figures 4.4-4.11, the average Shannon mutual information over time is shown for all three task-switching cost treatments. Each of these figures show a general trend that Shannon mutual information increases over time, therefore, division of labor increases as the task-switching cost increases. However, as referenced earlier, the temporal polyethism pattern has not changed substantially indicating that the lethality risks provide sufficient pressures against task-switching costs.

4.4 Discussion

When there are competing pressures of lethality risks associated with tasks and task-switching costs, we still observe the evolution of a temporal polyethism pattern in both two- and three-task trials. In two-task trials, we see that regardless of two different task-switching costs, replicates evolve a temporal polyethism pattern. In this case, risk dominates over task-switching costs. We see that as task-switching costs increase, however, average age in which an organism performs a task similarly increases (likely due to the penalty). Conversely, when the tasks are not associated with lethality pressures as in the control, the average age of task completion significantly decreases. There is not enough variety in tasks available to the colony for there to be a substantial increase in division of labor as measured by Shannon mutual information. In the three-task trials, we observe that the task-switching costs again do not affect the evolution of the temporal polyethism pattern in which riskier tasks are performed later in life. However, as task-switching costs increase, division of labor increases. In most cases, this increase was substantial compared with runs without task-switching costs.

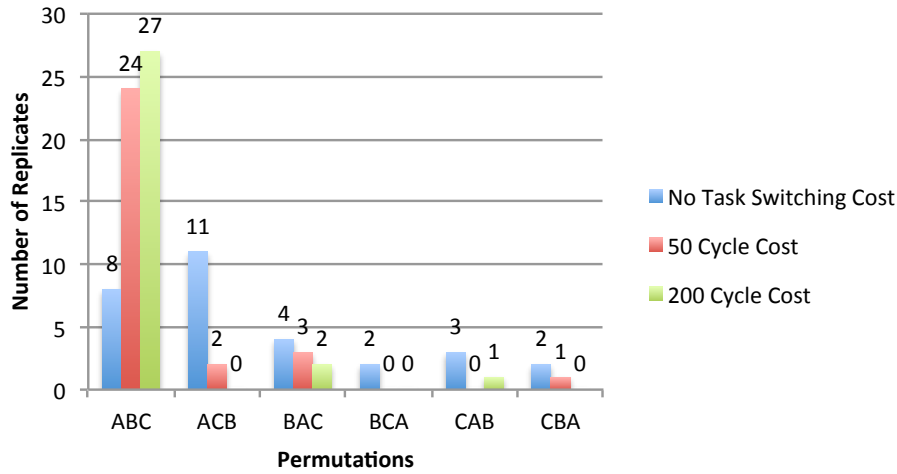


(a) Treatment: NOT is risky

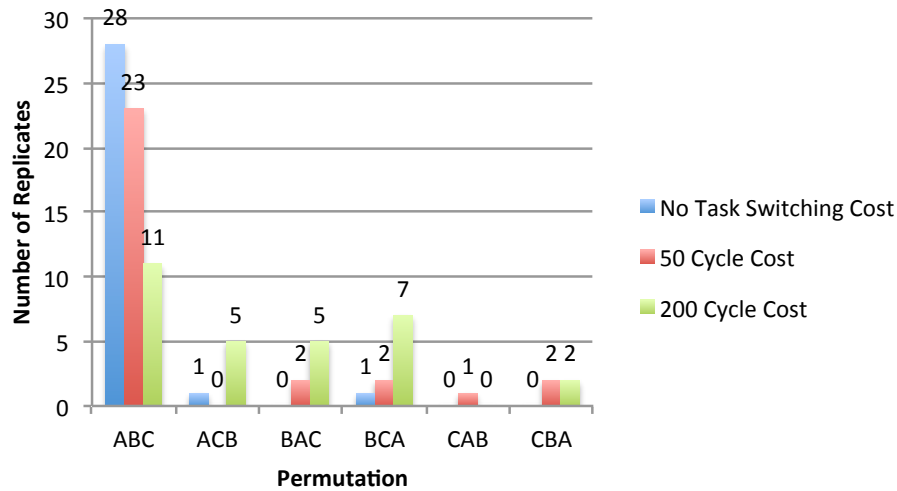


(b) Treatment: NAND is risky

Figure 4.2: The results of the two-task treatments, where task-switching penalties varied from no penalties to a low penalty of 50 cycles to a high penalty of 200 cycles associated with switching tasks. The y-axis of both plots is the number of replicates out of 30 that were able to perform the risky task later in life. The x-axis shows the results from two different ancestors: NOT-NAND and NAND-NOT. (a) results from when NOT is the 25% risky task and NAND is the safe task. (b) results from when NAND is the 25% risky task and NOT is the safe task. The key denotes the task-switching costs for each treatment. Selection for a temporal polyethism pattern is the same for each treatment regardless of task-switching cost (Fisher's exact test, $p < 0.05$).



(a) Treatment: All tasks have 0% risk



(b) Treatment: All tasks have 7% risk

Figure 4.3: The permutations of the mean age of task for the final population with no task-switching costs, with 50 cycles of task-switching costs, and 200 cycles of task-switching costs. The data shown is the task rearrangement from the original ancestor organism of ORNOT-NOT-NAND, denoted as ABC. The combination of the three letters indicate the task ordering by average age of task performance in the population at the end of the run as seen in Figure 3.4. We see that task-switching costs have a selective pressure for genome rearrangement. Alternatively, when every task has a 7% lethality, the selective pressure is removed and it is easier to favor colonies that have the same pattern as the ancestral organism.

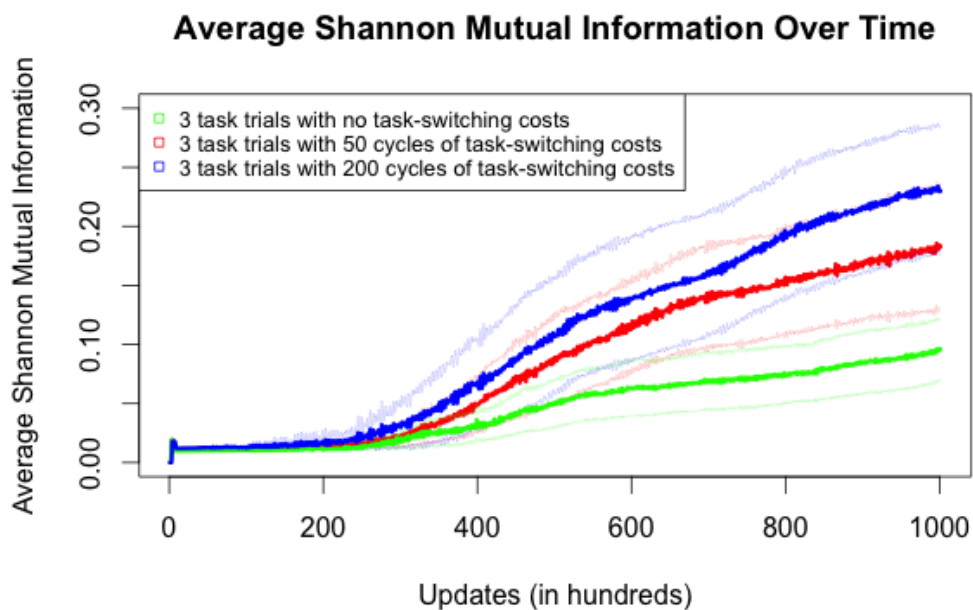


Figure 4.4: Average Shannon mutual information for treatment 0-7-15 from runs with ancestor organism ORNOT-NOT-NAND for three different task-switching costs. The green line represents runs that do not have any task-switching costs, the red line represents runs that have a task-switching cost of 50 cycles, and the blue line represents runs that have a task-switching cost of 200 cycles. Thin lines represent standard error. We observe that there is a significant increase in average Shannon diversity between runs without task-switching costs and both sets of runs with task-switching costs, respectively (Mann-Whitney U test, $p < 0.05$).

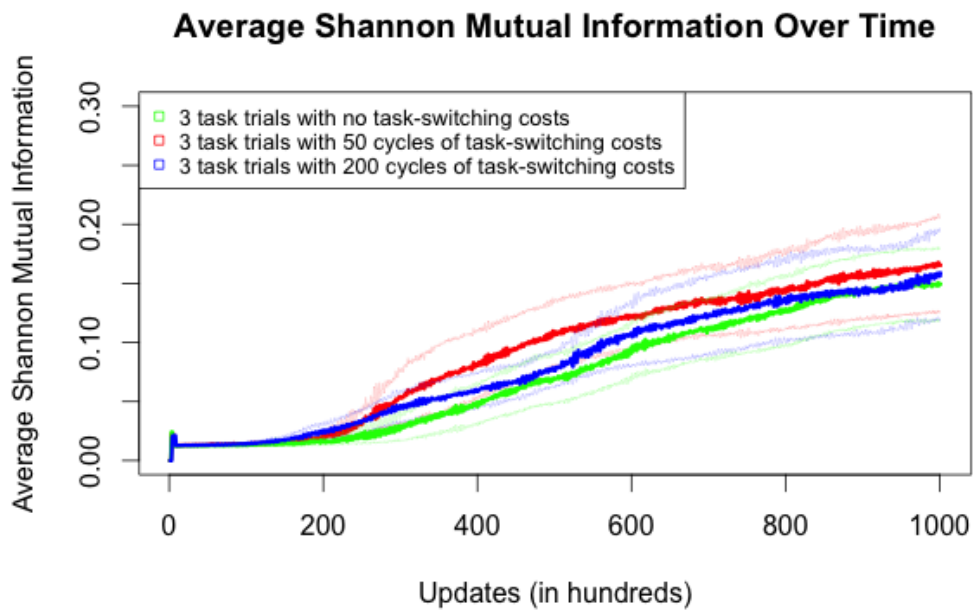


Figure 4.5: Average Shannon mutual information for treatment 0-15-7 from runs with ancestor organism ORNOT-NOT-NAND for three different task-switching costs. The green line represents runs that do not have any task-switching costs, the red line represents runs that have a task-switching cost of 50 cycles, and the blue line represents runs that have a task-switching cost of 200 cycles. Thin lines represent standard error. We observe that there is no significant increase in average Shannon diversity between runs without task-switching costs and runs with both 50 and 200 cycles of task-switching costs, respectively.

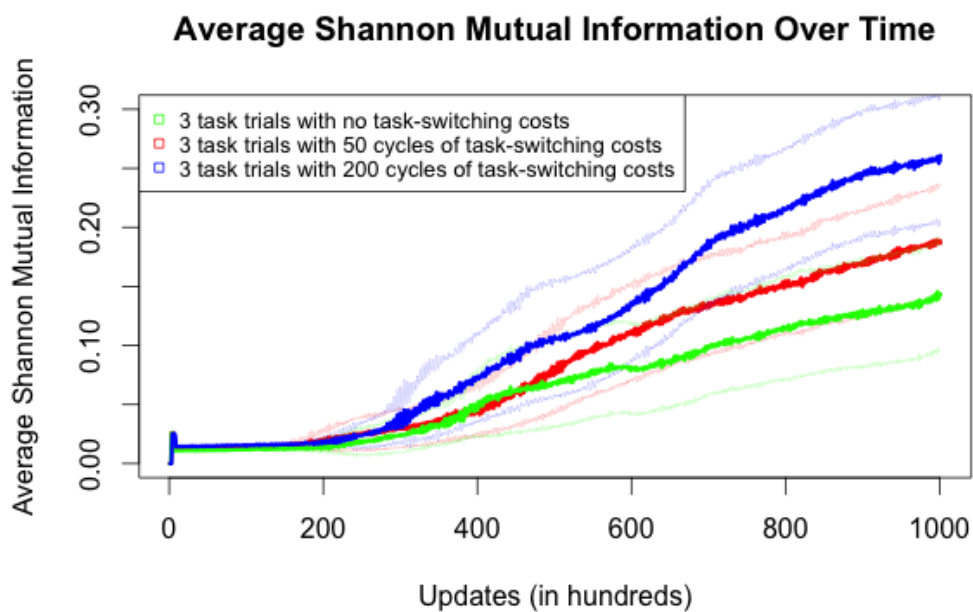


Figure 4.6: Average Shannon mutual information for treatment 7-0-15 from runs with ancestor organism ORNOT-NOT-NAND for three different task-switching costs. The green line represents runs that do not have any task-switching costs, the red line represents runs that have a task-switching cost of 50 cycles, and the blue line represents runs that have a task-switching cost of 200 cycles. Thin lines represent standard error. We observe that there is no significant increase in average Shannon diversity between runs without task-switching costs and runs with 50 cycles of task-switching costs. However, there is a significant increase in Shannon mutual information when a 200 cycle penalty is applied (Mann-Whitney U test, $p < 0.05$).

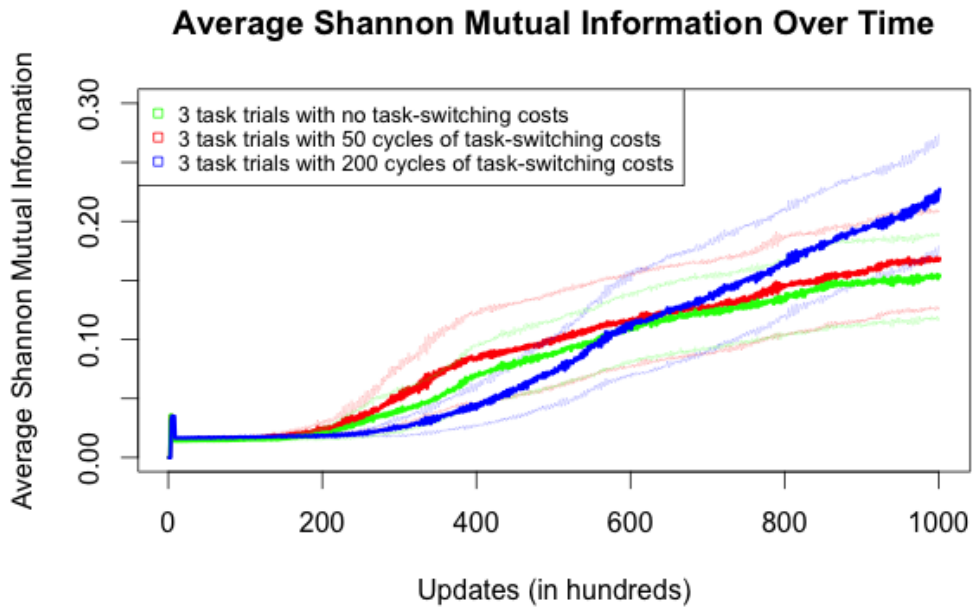


Figure 4.7: Average Shannon mutual information for treatment 7-15-0 from runs with ancestor organism ORNOT-NOT-NAND for three different task-switching costs. The green line represents runs that do not have any task-switching costs, the red line represents runs that have a task-switching cost of 50 cycles, and the blue line represents runs that have a task-switching cost of 200 cycles. Thin lines represent standard error. We observe that there is no significant increase in average Shannon diversity between runs without task-switching costs and runs with 50 cycles of task-switching costs. However, there is a significant increase in Shannon mutual information when a 200 cycle penalty is applied (Mann-Whitney U test, $p < 0.05$).

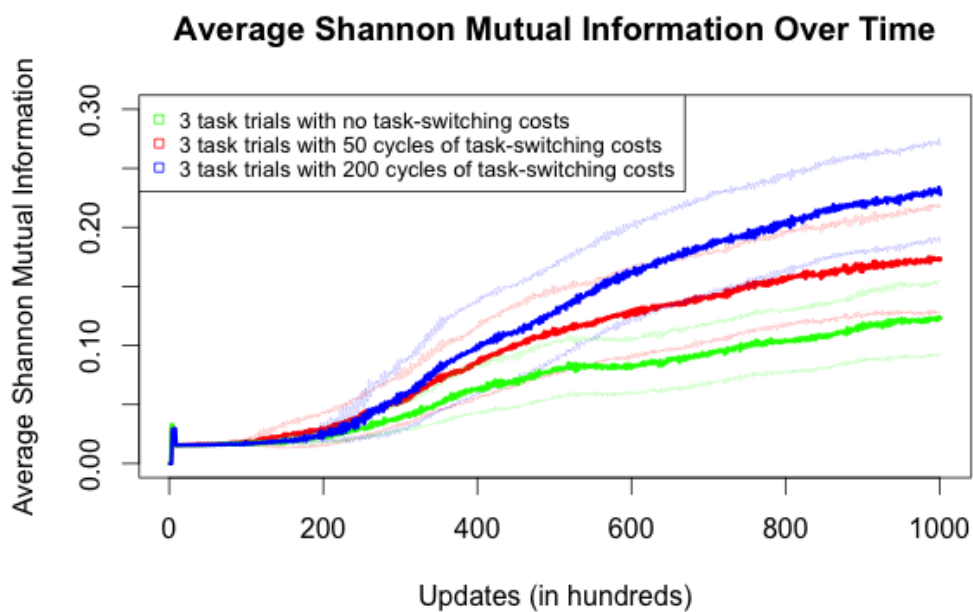


Figure 4.8: Average Shannon mutual information for treatment 15-0-7 from runs with ancestor organism ORNOT-NOT-NAND for three different task-switching costs. The green line represents runs that do not have any task-switching costs, the red line represents runs that have a task-switching cost of 50 cycles, and the blue line represents runs that have a task-switching cost of 200 cycles. Thin lines represent standard error. We observe that there is no significant increase in average Shannon diversity between runs without task-switching costs and runs with 50 cycles of task-switching costs. However, there is a significant increase in Shannon mutual information when a 200 cycle penalty is applied (Mann-Whitney U test, $p < 0.05$).

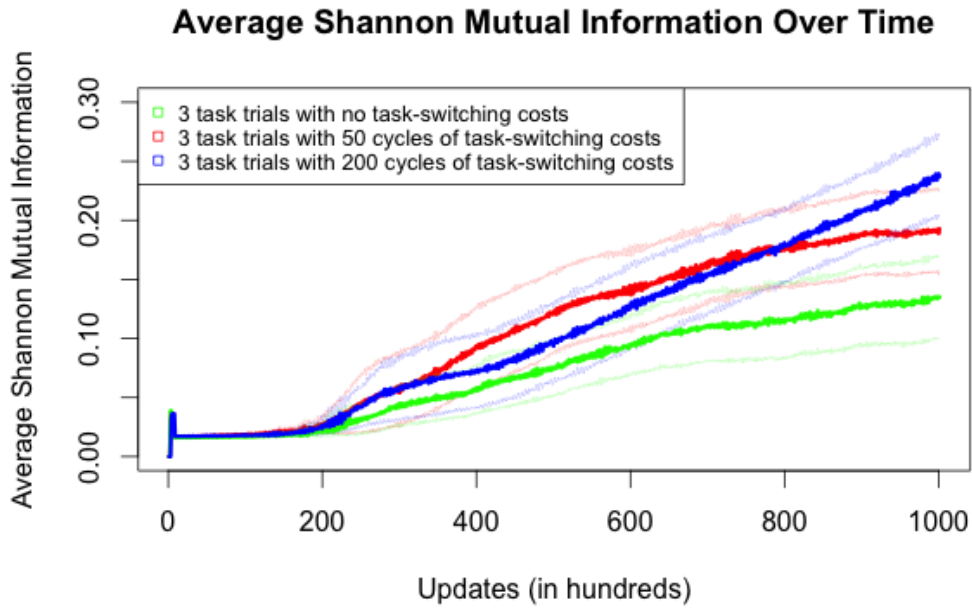


Figure 4.9: Average Shannon mutual information for treatment 15-7-0 from runs with ancestor organism ORNOT-NOT-NAND for three different task-switching costs. The green line represents runs that do not have any task-switching costs, the red line represents runs that have a task-switching cost of 50 cycles, and the blue line represents runs that have a task-switching cost of 200 cycles. Thin lines represent standard error. We observe that there is a significant increase in average Shannon diversity between runs without task-switching costs and both sets of runs with task-switching costs, respectively (Mann-Whitney U test, $p < 0.05$).

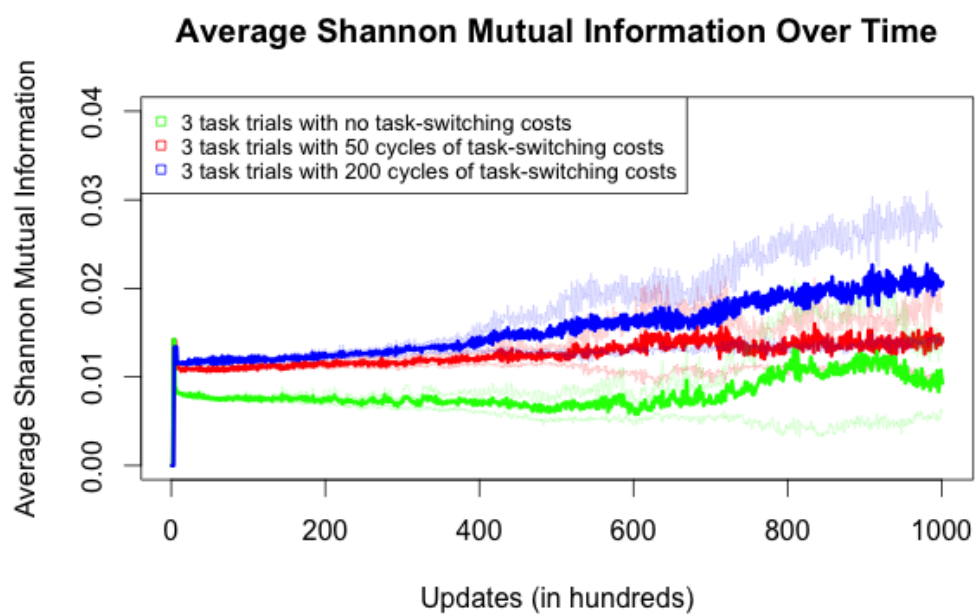


Figure 4.10: Average Shannon mutual information for treatment 0-0-0 from runs with ancestor organism ORNOT-NOT-NAND for three different task-switching costs. The green line represents runs that do not have any task-switching costs, the red line represents runs that have a task-switching cost of 50 cycles, and the blue line represents runs that have a task-switching cost of 200 cycles. Thin lines represent standard error. We observe that there is a significant increase in average Shannon diversity between runs without task-switching costs and both sets of runs with task-switching costs (Mann-Whitney U test, $p < 0.05$).

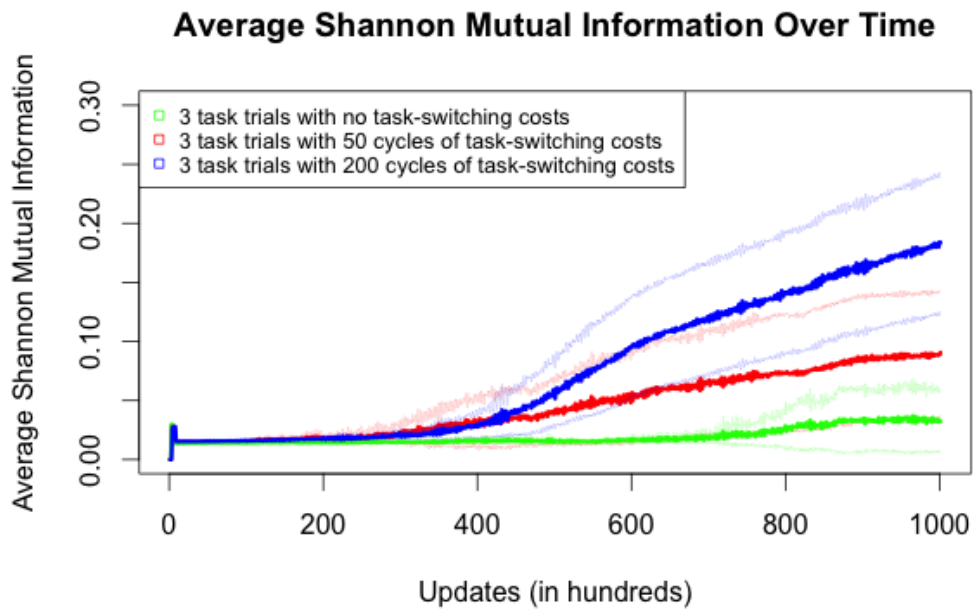


Figure 4.11: Average Shannon mutual information for treatment 7-7-7 from runs with ancestor organism ORNOT-NOT-NAND for three different task-switching costs. The green line represents runs that do not have any task-switching costs, the red line represents runs that have a task-switching cost of 50 cycles, and the blue line represents runs that have a task-switching cost of 200 cycles. Thin lines represent standard error. We observe that there is a significant increase in average Shannon diversity between runs without task-switching costs and both sets of runs with task-switching costs (Mann-Whitney U test, $p < 0.05$).

Chapter 5

CONCLUSIONS AND FUTURE WORKS**5.1 Conclusions**

In this thesis, we used Avida to explore the evolution of temporal polyethism. We see that the pressures resulting from associating tasks with lethality risks can lead to the evolution of temporal polyethism. We find that the magnitude of the risks associated with the tasks can affect results if organisms can rearrange their genome such that they complete the safer tasks earlier in life and the riskier tasks later in life. At higher risk levels, we see that evolution produces more colonies that have higher mean ages for completion of riskiest tasks, fitting a temporal-polyethism pattern in the two- and three-task trials. We discovered that while we did not have high enough selective pressure to favor the rearrangement of two tasks with lower risks (one having no risk at all, notably), at least two-thirds of trials will evolve such that the overall riskiest task is done later in life in the three task trials. These results demonstrate that pressures resulting from the relative riskiness of various tasks and aging is sufficient to favor the evolution of temporal polyethism. When we add competing pressures of task-switching penalties to the treatments, we still observe the evolution of temporal polyethism in both the two- and three-task treatments. Shannon mutual information was measured to observe the amount of division of labor in colonies. We see that as task-switching costs increase, the division of labor in colonies increase as well in the three-task trials.

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) or both. 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 [11]. 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 [22, 27].

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 [25]. 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 [25]. 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 [25]. Knocking down vitellogenin, a gene associated with JH, in bees similarly results in earlier task-switching to foraging and shorter lifespans [15]. 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 [24].

Within this thesis, we have demonstrated that associating tasks with lethality risks is sufficient for evolving a temporal-polyethism pattern. 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.

5.2 Future works

5.2.1 Simple model and other tweaks

In future work, we will refine our understanding of the the evolution of temporal polyethism and also will explore how factors other than risk interact to produce division of labor. To address the bias, we believe that simplifying our model would allow us to bypass task rearrangement difficulties. We created a model where each task was done by a simple instruction OP1, OP2, OP3. For organisms to switch the ordering of tasks, it would not require reordering multiple instructions as was the case earlier, but instead, only a single instruction would need to be moved. This would be as simple as a mutation that insert an instruction in a different place in the genome. We use the same structure as before with all of the same lethalties (0%, 7%, and 15%), 400 colonies of 25 organisms, and the same set of mutations (insertions, selections, etc.). We expect to see that in our controls where each task has the same lethality (either all 0% or all 7%), there would be equal probabilities for all permutations of the three tasks in terms of age ordering. This simple model would allow us to determine if there is a certain Avida-based complexity that is biasing our three-task results. These explorations are currently in progress.

In addition, we can see what the effect of increasing the number of generations. To do this, we will go from 100,000 updates to 500,000 updates. In the trials where colonies only had to do 150 of each task in order to replicate, we had many more generations in the end, and we saw that more replicates were able to evolve a temporal-polyethism pattern. We expect that if we have a similar but larger increase in generations, we will see a stronger pattern of temporal polyethism.

We will also see what the effect of changing the size of the new propagule after colony replication to be between only one organism and filling the colony completely. Biologically, new colonies rarely start with only one organism. An intermediate number will allow us to bypass the risk of having a certain percentage of all new colonies dying early on due to high lethality risks. In addition, it will let us see the dynamics of how more organisms in a starting colony can affect the evolution of division of labor in a colony.

5.2.2 Lifespan as a factor in temporal polyethism

To understand whether the increased threat of death with age is a factor in temporal polyethism, we will vary the distribution of random death within the population. Random death would be considered an organism prematurely dying in comparison to expected lifespan. Specifically, death within Avida is implemented as probability distribution. We will set this probability to be equal for all organisms of all ages. In doing so, death will be less correlated with age and thus, we will have reduced one of the possible pressures that plays a role in temporal polyethism. If age-based castes disappear, then there is empirical evidence that the risks associated with aging are a key factor in the evolution of temporal polyethism.

5.2.3 Perturbations to colony age structures

Similar to the study where bees turned into precocious foragers when older bees in the colony were removed[17], we want to see the effect of removing the oldest workers from colonies on the evolution of temporal polyethism. To ascertain this effect, we will configure Avida such that there will be events where the oldest 20% of the colony will be removed. Alternatively, we will also see the effect of removing the youngest 20% of the colony on the division-of-labor strategies that arise in the colony. These studies can mimic an external occurrence such as a mass killing of foraging bees or an attack on the hive wherein only older bees respond. This experiment can address concerns that an age-based division-of-labor strategy is not flexible enough to account for natural disasters.

5.2.4 Effect of colony size on division of labor strategies

As evidenced earlier in Chapter 3, we see that the evolution of temporal polyethism is favored when there is an intermediate colony size. In Chapter 3, we tried three different colony sizes - 25, 50, and 250 organisms. We observed that 25 organisms per colony may have been too small, whereas, 250 organisms per colony was too big. In the future, we would like to look at how a variety of colony sizes affects the evolution of division-of-labor strategies. The analog in biology would be that a smaller colony may find it more beneficial

for everyone in the colony to be able to do every task in case of death of other colony members. Conversely, a larger colony may find it more favorable for subsets of the colony to specialize on tasks so there is not as much task repetition amongst members. We can use Avida to determine how colony size competes with lethality risks as pressures for the evolution of division-of-labor strategy in a colony.

5.2.5 Differing amounts of tasks needed for the colony

In our model, we unrealistically assumed that each colony would need to do the same amount of each task. In nature, foraging is considered a sink for work [27] in that there will always be work needed in that area. To address this, we will use Avida to require different amounts of tasks for colony replication. For example, we can set it so that each colony only needs 100 successful completions of the least risky task but they also need 200 of a moderately risky task and 500 of the riskiest task. In this case, we expect to see the evolution of a genomic structure where organisms complete the least risky and moderately risky tasks first and then they loop over the riskiest task until their death as we see in the case study in Chapter 2. We can do all permutations of this as well—it could be necessary that the least risky task needs 500 successful completions of the task whereas the riskiest task only needs 100. This would elucidate how the amount of tasks needed for the colony affects the division-of-labor pattern used by the colony.

5.2.6 Task-switching model expansions

As seen earlier in Chapter 4, we have preliminary results for the effect of task-switching costs on the evolution of temporal polyethism. To expand upon this, we would like to assess the effect of a variety of task-switching costs. We showed data from task-switching costs of both a low cost of 50 cycles and a high cost of 200 cycles. We want to try a variety of other task-switching costs to see when this pressure is enough to overcome the competing pressure of lethality risks.

In addition, the effect of different task-switching costs based on age would have a nice analog to task regulation by hormones. For example, a younger worker would have to

expend more energy to switch to a task that it was not developmentally ready for at the time. An older worker, having had more experience doing previous tasks, would have a lower cost for switching tasks. By varying the task-switching costs based on age, we could verify the effect of an age-based punishment on the evolution of temporal polyethism.

5.2.7 Spatial task-switching costs

To study the foraging-for-work model, we want to add an abstract spatial structure to the tasks. We created a bullseye-like structure where the nest is in the center and organisms are born in the middle as seen in Figure 5.1. In the middle, the organisms can do the task NOT in this example. They have to move outward to do other tasks, and as they switch to a new task, they are penalized with a task-switching cost proportional to the amount of space they moved. For example, in Figure 5.1, if an organism switches from task NOT to NAND, there is one task-switching penalty of 50 cycles. If the organism switches from task NOT to ORNOT, organism is penalized with two task-switching costs, totaling 100 cycles.

In this study, permutations of starting organisms with all permutations of risks for each task and all permutations of spatiality of tasks for a total of 8640 runs. The spatial task permutations are shown in Figure 5.2. This full combinatorial design was created to ensure that there was not anything inherent about the order of tasks themselves. This foraging-for-work task-switching model addresses the limitations of Tofts' model in that his 'ants' could move between tasks without any penalty. Preliminary results indicate that spatial task-switching costs may be a substantial competing pressure to lethality risks in the evolution of temporal polyethism.

5.2.8 Competitions between division of labor strategies

A central question is why is temporal polyethism a prevalent strategy for colonies over specialization? To address this, we will take successful colonies that were evolved under different conditions and compete them. For example, we will take a successful colony from a treatment with no lethality and see how it fares in its original no-risk environment against a colony that was evolved under differing lethality risks associated with tasks. We will also

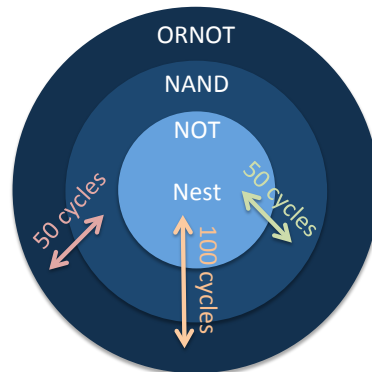


Figure 5.1: An example nest showing the spatial location of three tasks. Organisms are born in the center of the nest, which in this case is NOT. When organisms move outward one layer in the nest to transition to a new task, they are penalized with a 50-cycle task-switching cost. When organisms move two layers to transition to a new task, they are penalized with twice the original task-switching cost for a total of 100 cycles.

see how a colony that evolved without task-switching costs will do when it is placed in an environment that has these costs. There are a variety of competitions that we can try to assess their effect on division-of-labor strategies.

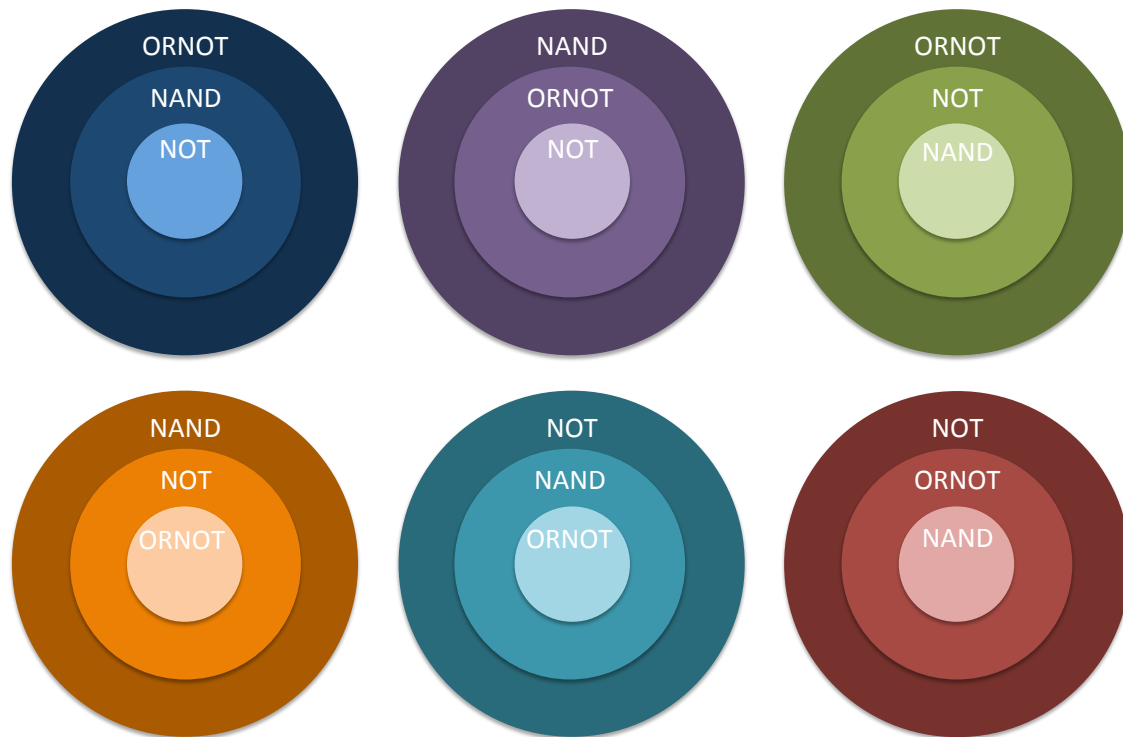


Figure 5.2: All possible nest permutations for task arrangements are shown. Organisms are born in the center of each nest, and moving outward to different tasks is associated with a task-switching penalty. The six nest structures will be used to ensure there is no bias from the arrangement of tasks in the nest.

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