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A Review of Evolution, Behavior, and Vision with an Experimental Evolution Study on Color Vision in Drosophila melanogaster

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Dedication

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Abstract

The first chapter of this thesis is to take a piece by piece look at the factors that contributed to the experimental evolution study that will be discussed in Chapter 2. Behavior, how that can affect experimental studies, and how biases can affect sensory systems and preference in subject species. Specifically visual sensory systems are described in detail, from the possible evolutionary histories, to major components that contribute to eye structure, form, and/or abilities. We discuss how to define color vision, and what are the prerequisites for color vision in species.

Key Words: Bias, Color Vision, *Drosophila*, Evolutionary Economics, Experimental Evolution, Proximate Causation, Ultimate Causation, Vertebrate

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Definitions

1) **Adaptation**- When an organism becomes better able to live in its habitats via an evolutionary process (Bateson & Laland, 2014; Blackiston, 2007; Dosi & Nelson, 1994; Dukas, 2008; Garland & Kelly, 2006; Kuhn, et al., 2003; Shettleworth, 2010).

2) **Color Constancy**- A perceived color remains constant despite changing lighting environments (Arnold, 2010; Blackiston, 2007; Chittka, et al., 2014; Fischbach, 1979; Lotto & Purves 2002).

3) **Color Vision**- is the ability of an organism to use its visual sensory organs (which contain two or more photoreceptors) and the corresponding neural systems to discriminate wavelengths and categorize objects based on color (Chittka, et al., 2014; Deeb & Motulsky, 1996; Kelber, Vorobyev & Osorio, 2003; Lunau & Maier, 1995; Renoult, Kelber, & Schaefer, 2015; Rushton, 1972).

4) **Discrimination**- The ability to distinguish and quantify differences in two or more things (Akre & Johnsen, 2014; Bicker & Reichert, 1978; Giurfa, 2004; Pashler & Wixted, 2002; Renoult, Kelber, & Schaefer, 2015; Shettleworth, 2010).

5) **Experimental Evolution**- Garland & Rose (2009) "research in which populations are studied across multiple generations under defined and reproducible conditions, whether in the lab or in nature" (Bennett 2003; Chippendale, 2006; Garland, 2003; Garland & Kelly, 2006; Kawecki, et al., 2012; Swallow & Garland, 2005).

6) **Evolutionary Economics**- the study of the processes that transform the human economies (Dosi & Nelson, 1994).

7) **Homeobox**- a family of genes (Dictonary.com).

8) **Ommatidia**- Each optical unit of the compound eye (Arnold, 2010; Beersma, Stavenga, & Kuiper, 1975; Bicker & Reichert, 1978).

9) **Opsin**- The light-sensitive proteins in photoreceptor cells that convert photons to electrochemical signals (Kelber, Vorobyev & Osorio, 2003; Surridge, Osorio & Mundy, 2003).

10) **Perceptual Bias**- The innate preference in a signaling system that exists before sexual selection occurs, to drive selection and divergent adaptation (Endler & Basolo, 1998; Raine & Chittka, 2007; Ryan & Cummings, 2013; Shettleworth, 2010).

11) **Phenotypic Plasticity**- A single genotype's ability to express multiple phenotypes depending on the environment (Garland & Kelly, 2006; Snell-Rood & Papaj, 2009; Shettleworth, 2010).

12) **Photopigment-** the chemical state of a pigment that changes based on illumination (Deeb & Motulsky, 1996; Goyret, et al., 2008; Kelber, Vorobyev & Osorio, 2003; Rushton, 1972; Ryan & Cummings, 2013; Surridge, Osorio & Mundy, 2003).

13) **Photoreceptor**- A specialized neuron that uses the converted photon-electrochemical signals to simulate biological processes (Bicker & Reichert, 1978; Deeb & Motulsky, 1996; Frederiksen, Wcislo & Warrant, 2008; Kelber, Vorobyev & Osorio, 2003; Lunau & Maier, 1995; Paulk, Millard & von Swinderen, 2013; Renoult, Kelber, & Schaefer, 2015; Ryan & Cummings, 2013; Surridge, Osorio & Mundy, 2003).

14) **Phototaxis**- The movement of a mobile organism in response to light (Bicker & Reichert, 1978; Blackiston, 2007; Gao, et al., 2008; Kelber, Vorobyev & Osorio, 2003; Paulk, Millard & von Swinderen, 2013).

15) **Proximate Causation**- The event closest to an end result that is observed to have caused the end result (Alcock & Sherman, 1994; Bateson & Laland, 2014; Shettleworth, 2010).

16) **Psychophysics**- The psychological study of the relationships between physical stimuli and mental processes (Greenfield, 2014; Pashler & Wixted, 2002; Renoult, Kelber, & Schaefer, 2015).

17) **Sensory Ecology**- Information obtained by organisms about their environment, including how information is obtained, and why the information is useful to the organism (Goyret, et al., 2008; Shettleworth, 2010).

18) **Spectral Sensitivity**- The ability to detect a signal with relative efficiency and frequency (Goyret, et al., 2008; Hernandez de Salomon & Spatz, 1983; Kelber, Vorobyev & Osorio, 2003; Lunau & Maier, 1995; Rushton, 1972; Surridge, Osorio & Mundy, 2003; Vorobyev & Osorio, 1998).

19) **Ultimate Causation**- A higher level cause event that can precipitate an observed end event, but is not readily observed as the Proximate Causation (Alcock & Sherman, 1994; Bateson & Laland, 2014).

Chapter 1: Everyone's a Little Bit Biased: A Review of Experimental Evolution as it Relates to Visual Ecology and Color Vision

1.0. Introduction

Over the centuries of vision research, no question has been more vexing to scientists than the idea that colors are not perceived the same way among individuals in a population. Researchers have been able to document wavelengths of light and record the sensitivities of the receptors with the neural processing networks of the eyes across many species. The genes that encode the receptors have been mapped and standard tests for human color vision are given in schools. Yet, it may never be possible to completely document that one person's "green" is not another's "red". The receptor cells can be excited by the same wavelength, processed, and interpreted along the same neural network, and referenced by previous experiences of the same color; but if somehow the receptors switched, or the experiences change, or the brain of one individual processes the receptor of the other may see an inverted visual spectrum, or that spectrum may be skewed differently.

The inherent problem with this example is that most humans (and a majority of other animals and insects) see colors in novel ways. From color vision defects in humans, to sexual dimorphism in new world monkeys (NWM) (Melin, et al., 2006) and insects (Hilbrant, et al., 2014; Ogawa, et al., 2012), the world is a different visual experience for every being with the ability to see. From the receptors that can detect specific wavelengths of light, to the inherent experience by which the wavelength is processed, every part of color vision is biased genetically, morphologically, and perceptually.

While the context of perception of color vision is fascinating, the overall benefit of vision and color vision is enhanced by the tonnage of knowledge obtained to understand how vision functions, how it evolved, and how vision is defined. This

information may someday answer that impossible question. For is it not the creed of science to answer those impossible questions?

2.0. Behavior

An explanation of behavior must include comprehensive arguments of learning, cognition, and evolution. Behavior is a direct reflection of an organism's sensory, motor, motivational, and cognitive forces reacting to a signal, a stimuli, or the environment (Endler, 1993; Lotto & Chittka, 2005; Rockwell, 1978; Shettleworth, 2010). This behavior can be innate, learned (Dukas, 2013; Giurfa, 2004; Weiss & Papaj, 2003), or altered based on life history and evolutionary history changes. As an example; an animal is hungry, where the internal system of an empty stomach relays a "get sustenance" signal, the behavior directly caused by that signal is to "stop being hungry" and the individual forages for food of some kind (Shettleworth, 2010). The direct cost of not preforming the behavior is eventual death, but increase in "need to get energy" over the short term. So the end goal of a behavior is the continued existence and well-being of the individual performing it, and that optimizing the behavior is adaptive.

The behavioral systems that arise from these co-mingled signal-to-behavior events are (theoretically) optimized machines. The system's function is to complete a specialized goal (sex, fear, etc.). These systems are affected by proximal causations, stimulants, perceptions, and environmental factors that are prioritized in a centralized network to coordinate the appropriate internal and external relays for the behavioral system to function. Within each individual there are multiple behavioral systems; and each system is affected by varying external and internal cues (Vorobyev, et al., 2001).

These multiple systems are prioritized in a "secondary" hierarchy, which further affects a single behavioral system by life history biases of one behavior system's priority over another. Which is to say the act of running away from a lion to avoid being eaten would take priority over being moderately without food for the moment. These innate biases are time dependent, and can be environment dependent (Endler, 1993; Kunze & Gumbert, 2001; Mery & Kawecki, 2004b; Miller, et al., 2011; Shettleworth, 2010; Tang & Guo, 2001). This will be further discussed in section 3.2.

Behavior is a continually shifting, living, and active description of an animal's reaction to environmental cues (Chapman, et al., 2010; Shettleworth, 2010) and to the diversification of genes involved in higher behavioral function due to genetic and phenotypic plasticity (Chen, et al., 2012). To understand why behavior is hard to compactly define, the general terminology and mechanisms must be observed.

2.1. Proximate & ultimate causations.

The creation of a bias or a behavior (or generally anything observable in evolution) is based on both the most immediate (current) cause, and the overall cause for the behavior or bias (Mayr, 1988). The immediate cause or internal mechanisms of the behavior is a Proximate Cause, and the overall consequences or causes of behavior is an Ultimate Cause (Alcock-Sherman, 1994; Chittka, et al., 2012). Both of these causes were taken from Mayr (1954) and extrapolated to Tinbergen's four questions of animal behavior, which helped translate the confusing sections of Mayr to distinct sections moving from past to present events (Bateson & Laland, 2014; Shettleworth, 2010; Tinbergen, 1963). These four questions are used to determine if proximate or ultimate

causation is being observed and are as follows: What is the causation of the behavior? How does the behavior come about from experience and/or genetic makeup? Why/how does this behavior increase evolutionary benefit? How did the behavior evolve? These questions have been slightly modified to represent modern vocabulary, as Tinbergen's terminology is currently outdated as some terms have changed meaning in the last half century (Bateson & Laland, 2010; Stevens, 2013).

These four questions were grouped in sets of two in each category which could go and answer Proximate and Ultimate Causations (Mayr, 1982a; Nesse, 2013), wherein the immediate reasoning to an action or behavior is considered a Proximate Causation (Mayr, 1988). This is as simple to explain as a bias or conditioning event. While there may be other reasons for the behavior, the most immediate and obvious bias or cause is the proximate. The Functional or Ultimate Causation is the evolutionarily benefit end of the behavior (Cuthill, 2005; Hogan, 2005; Stevens, 2013).

There is an ongoing push by behavior scientist that grouping the four questions to two categories loses the process by which Tinbergen meant these questions to be used; to explain a behavior entirely (Nesse, 2013). A table has been made combining the original four questions with the causation categories; see Nesse, 2013-Figure 1 for an example of the chart denoting the categories. This table was created to try and simplify the growing evolutionary factors that can shape a species into its current form, current terminology, and attempts to reduce future confusion.

The argument being made is that the key to understanding behavior and the Causations, is to answer all of Tinbergen's questions (and possibly a fifth question postulated for culture by Kacelnik (2006) (Bateson & Laland, 2010)). As recent behavior

of choice, theory of mind, and decision making experiments offer economic value to a multitude of options a species (or individual) may make. This requires a level of cognitive ability (Tinbergen, 1951; 1959) - or proximate cause- that necessitates the individual to be aware of alternate choices and can weigh the different choices against each other for optimal choice selection. This may also require the individual to sometimes be aware of other individuals in the experiment also having the same choices available to them and reacting accordingly (Shettleworth, 2010).

The lesson is to answer all of the questions put forth by Tinbergen before coming to a conclusion about a population's behavior. Additionally, a warning is presented that the act of observing a population in the wild may change the behavior of the observed population, and that experiments run in a lab may express behaviors that would not be observed in the wild (Tinbergen, 1951; 1959). These precautionary examples can influence the development of an experimental setup if not properly adhered to.

The complexity in the studying of behavior and the experimental behaviors (Boake, 1994) is that: 1) Behavior is sensitive to small and (sometimes) uncontrollable variations in the environment, 2) animals emotional states matter, 3) influenced by learning (memory, past experience, past environments, past behaviors) 4) low repeatability of behavior (based on ancestral environment and experience), 5) assays to fix low reproducibility can have problems on the type of assay chosen to run, 6) assays try to reduce starting complexity of behaviors down to a few behaviors that are measurable, 7) a highly complex behavior being selected can be assayed in a variety of ways (Battesti, et al., 2012; Endler, 1993). "Behavior evolves first" is assumed to predate sexual selection and innate biases before complexity of behaviors develop (Bloomberg,

Garland & Ives, 2003; Mayr, 1958). Though selecting for preferences in experimental evolution experiments can create a problem because changing behavior in one aspect can change another because some genetic coupling in behaviors has been observed (Abed-Vieillard, et al., 2013; Bullock, 1997; Rauser, Mueller, & Rose, 2003; Roff & Fairbairn, 2001).

For testing evolution in a lab there are 3 basic approaches of experimental methods: 1) artificial selection (Simoes, et al., 2007); this explains proximate and ultimate underlying mechanisms in how behavior evolves, but will lack an adaptive explanation of the behavior, 2) mass selection; dividing up a population based on behavior divergence, or 3) laboratory natural selection (Garland, 2003); no behavior directly evolved here yet, but it is implied and inferred for other experiments; characteristics are selected to contribute to the next generation over others.

2.2. Experimental evolution.

Once Tinbergen's questions have been studied, sometimes (in order to answer them to the fullest capacity) an evolutionary experiment has to be performed. Evolutionary theories, while supported by literal tons of empirical data, are only one type of research model, and experimental evolution studies can attempt to record evolution in a smaller time frame than Evolution by Natural Selection (Bullock, 1997; Kawecki, et al., 2012). Simplified experimental evolution is the controlled experimental environment where the study of evolutionary changes on an experimental population can be observed in real time once a selective pressure is imposed by the researcher. Kawecki (et al., 2012) simplified this as "laboratory natural selection" experiments.

To begin an experimental evolution trial, a series of reproducing populations in a novel environment (with a control in the ancestral environment) is required (Gould, 1990). This is structured for a laboratory environment- not the field or real environment; with the downsides of this construct being the limiting of which species can be used for the experiments (a large, rapidly reproducing population is necessary), and a lack of realism to ecological standards will be persistent.

Populations that are able to be used in these experiments (Endler, 1986) are lacking, but those few species have statistical replication benefits. In the event that the species are used though, the correlation verses causation fallacy can arise if proper methods are not used, or if improper theories have been applied (Garland & Adolph, 1994). Once the appropriate species/population for the experiment has been chosen, the application of the study is usually directed towards four major groupings (Kawecki, et al., 2012).

First, there are comparative studies where the experimental population is observed against models of evolutionary theories. These 'proof of principle studies' (Kawecki, et al., 2012) test sexual selection, genetic drift, and reproductive isolation as evolutionary processes of speciation against the observed populations being experimented on. This system is flawed, as experimental setups to test some theoretical models of evolution do not exist, or have not been constructed properly as to answer unequivocally that the theoretical model was approved or disproved (Garland & Kelly, 2006; Kawecki, et al., 2012).

The second type of experimental evolution study examines traits within a natural population. These traits would be quantified into heritable traits, variable traits, traits

under selective pressure, and fitness of the traits within and between replicating populations. As these traits can be affected by mutations that alter it any of its qualities, mutational studies are also considered experimental evolution studies. These mutation experiments observe how the mutation(s) alter trait fitness, and other factors. Thus mutation rates within an experimental population's genome are calculated, and observed for adaptation effects on the populations (Garland & Kelly, 2006; Kawecki, et al., 2012; Morange, 2011).

Additionally, adaptation effects under specific environmental pressures is the third type of experimental evolution category. Generally called adaptive studies that observe a population under a controlled ecological constraint (i.e., nutrition, competition, stress, etc.), or under no specified constraint with the experimental population having a natural allele frequency (random). Either system can be used to do any combination of the following: infer the fitness of an adaptive trait, observe how phenotypes drift over time, or determine if other traits evolve (those unexpected results) outside of the original phenotypic alleles (Garland & Kelly, 2006; Kawecki, et al., 2012).

The last general category of evolutionary experiments studies the trade-offs of adaptations, phenotypic plasticity, and constraints inherent in the experimental population. Observing and measuring changes in trait preferences, fitness, or determining ecological constraints on learning within and between populations can determine behavioral biases, innate learning, or sensory system preferences which further explain the life histories of the species (Garland & Kelly, 2006; Kawecki, et al., 2012).

An extension of the four groups of experimental evolution tests is the "long-term" experiments. The length of these experiments are constrained by the type of species being

observed, the generational turnover rate of the species, and the resources to maintain the experiment and the population (how small an individual is, how quickly the next generation will mature and the food needed to maintain it) can cut down the length of an experiment from years to months before the research cost is expended (Kawecki, et al., 2012).

One long term experimental evolution study has been occurring since 1988 (Fox & Lenski, 2015; Kawecki, et al., 2012). *E. coli* in twelve replicates have been used to determine how rates of evolution vary over time; which evolutionary changes are reliable in separate populations under identical environments; relation between phenotypic and genetic levels over time. Each of the 12 populations are grown on minimal growth media for one day (6.64 generations per day); then every day 1% of the population is transferred to fresh media. Every 75 days (500 generations) a large proportion of the population is frozen for a "frozen fossil record" (Pennisi, 2013).

In general these lengthy experiments will usually need to alter their original platforms of observations to answer questions as they arise, or handle unforsean complications to the original design. Back to the *E. coli* experiment, in 1988 the initial focus of the experiment was to obtain observations for the dynamics of adaptations and the likely divergence of the original 12 replicate populations via fitness (Kawecki, et al., 2012). As the experiment logged observations, and maintained records, new questions emerged from ability to observe evolution over such a time scale. New evolutionary theories of adaptation were developed, so the original experiment modified its criteria to use the new models- some novel like epigenetics. Better observational equipment became readily available (and were cheaper), so the methods of the experiment were adapted to

use the new inventions and prevent researcher biases. Genomic research and observation became easier to preform and was relatively cheap to perform on populations, and, additionally, comparison of genomes between populations was more robust as genome libraries are being added to constantly. So genetic variation could now be observed on top of morphological variations, and mutations could be mapped (Kawecki, et al., 2012). Most experiments do not have to alter the methods over time, as they would not run long enough to necessitate that need.

The choice of the organism to study is much more static in the development of an evolution experiment. The model species should be assessed on convenience to the experimenter; using a model species over a novel species could benefit the researcher due to the aviablility of more information from different fields of studies related to the model species. Model systems are more likely to have genomic information to share, and species mutants could be available to purchase. Though the Wild-type lab population could not be reflective of natural populations (Kawecki, et al., 2012).

After the species for the experiment has been decided upon, the hypothesis testing can be constructed. Usually these experiments are structured around multiple population sets (replicates) of the base population of the species being tested. The species' ancestral genotype, or starting genotype at the beginning of the experiment is consistent between all the replicate populations. Each of these replicates will be subject to different treatments or selective regimes. The *E. coli* experiment from earlier had twelve separate bottles at the start of the experiment, and each bottle (replicate) had a population of *E. coli* that was genetically similar to each other. While the *E. coli* experiment does not conduct overt selective pressure on any of the replicate populations, genetic drift will still

act on the isolated populations causing genetic divergence between the species, which occurs only from the pre-existing genetic variation the base population had to start with (Kawecki, et al., 2012).

Kawecki (et al., 2012) argues that control replicates that are supposed to exist under the ancestral base population's environment rarely do exist under the standard conditions, so these controls should be done away with. While they are correct that any genomic data can be compared to the base population's genome at any time (if it's genome was already mapped), thus a comparison of ancestral genomic data that is readily handy could coopt the need for a control group in the experiment, and the blanket statement of "no controls alongside selection replicates" is flawed. Under the narrow scope of the "genetic drift" hypothesis testing, a control replicate would be unnecessary as no overt selection pressure is taking place, and a control that would show "No- overt selection pressure" results is redundant. However, any other experimental evolution study that does exert a selective pressure should have a "Genetic Drift" control. For example, in my experiments, as I was selecting for the evolution of color preferences in my 'Selection' replicates, I had two "Control" replicates that would be useful to compare my 'Selected' lines to, so as to disprove that genetic drift is the reason for my end of experiment results. To show the selective pressure occurred without genetic drift a "genetic drift control" would be worth consulting by experiment's end.

And once the experiment is over, the different evolutionary theories should be assessed for typical and not typical drives. Unique systems that may arise include supernormal stimuli preferences, or phenotypic/behavioral plasticity.

2.2.1. Phenotypic plasticity.

Four hypothesis of directional natural selection on phenotypic plasticity (which are not mutually exclusive from each other): 1) if higher quantities of a selected trait are favored within a population with additive genetic variance, then the average number of individuals with the selected trait will increase steadily from generation to generation, excepting traits that are correlated functionally, but selected upon separately. 2) Favored alleles would possess pleiotropic effects, and those effects would cascade to influence and evolve the components of complex phenotypes. An example of this hypothesis is if high energy foraging alleles in individuals were favored by selection to encourage food scavenging, the alleles that increased high activity for locomotor function would be directly favored, and peripheral alleles that increased high activity would also be favored to a lesser extent. The architecture of these traits are directly involved with the favored effects, and thus evolves to become more constant (phenotypically and genetically) trough multivariate selection, which amplifies the selection on the plastic phenotype to further force its evolution to facilitate adaptive radiation. 3) Again, starting with favored alleles within a population, the enforcement of directional selection on the genetic trait will cause a stepwise phenotypic dominance spectrum in the Direction of the selective pressure. Using the example from before, the foraging alleles in individuals would be selected upon in an upwards direction towards the high energy phenotype. To simplify the negative energy phenotype, the neutral energy phenotype, and the high energy phenotypes exist for the foraging alleles, the direction of the selective pressure would increase up the phenotypic line for - negative energy phenotype, the neutral energy phenotype, and the high energy phenotype- in a spectrum. 4) If a selective agent is

imposing ‘stress’ on a population for any recordable amount of time, then the rate of plasticity of the population should evolve directionally towards adaptation. The plasticity of traits in a population being evolved should become more constant (less variable) as the selective agent continues over time (Garland & Kelly, 2006).

The unique ability for the phenotypes of an individual to be directly altered due to the environment without altering the genetic makeup. A somewhat better definition was described in Garland & Kelly (2006): “the ability of one genotype to produce more than one phenotype when exposed to different environments”. This is also called “compensatory phenotypic plasticity” (Chapman, et al., 2010; Miller, et al., 2011). The sequence of events that result in the plasticity of the individual can follow the component steps of a) a single thing in the environment changes, b) the individual senses (a), c) the genes expressed are altered because of (b), and d) (c) produces a phenotype that can be observed. This also may require amplification of the genes then being expressed. In experimental evolution studies plasticity is heritable, is quick to respond to selective pressures, and has multiple loci determining its expression. And, in general, when plasticity occurs it cannot be reverted during the lifespan of the individual (Garland & Kelly, 2006; Kent, 2009).

Plasticity is most favored (while adhering to special variability, optimality, quantitative genetic and gamic models) when: “1)inter-habitat variability is high, 2) all habitats are equally regular, 2) selection acts strongly across habitats, 4) the environmental cue dependent phenotype is correlated with environment of selection, and 5) habitat selection is correlated with trait plasticity” (Garland & Kelly, 2006). Plasticity should be most favored when alternative environments occur in a predictable

set quantities- if there are five habitats (1 through 5) that individual A from species X can survive in with relatively high fitness, and there are 2 additional habitats (6 & 7) that "A" could live in with some phenotypic alterations to improve fitness; the predicted quantities of the environments would remain the same even if Habitats 1 and 4 took on the environments that Habitats 6 & 7 had, the set values would dictate that Habitats 6 & 7 then take on the original environmental conditions of Habitats 1 & 4, so we have 5 goof fit environments and two almost fit environments for Individual "A" no matter what. This perfect oscillation of environments is almost impossible to achieve with any habitats in the field (Burbridge, et al., 2014; Glanzman, 2010; Snell-Rood & Papaj, 2009; Weiss, 1997).

As explained in Garland & Kelly, (2006) above, a plastic phenotype can evolve through to adaptive radiation and in constant environments it would be expected that plasticity would diminish as variability has a cost to maintain. That cost in a steady environment would prefer to refocus that cost to optimizing a constant phenotype to match the constant habitat. Yet many studies have shown that even species that live in nearly constant environments still retain the plasticity of their phenotypes when introduced to a rare or novel environment. This implies that the operating cost to maintain plasticity mechanisms is lower than the cost to fix traits under steady environmental habitats. Snell-Rood & Papaj, (2009) explained how biases would reduce operating costs in a fixed environment, as the bias predisposes the individual to preform instinctually according to the set choice in the fixed environment, the operating cost to alter this bias –learning- would be the plastic mechanisms if a rare environment is encountered (Dukas, 2013).

"Behavioral genetic techniques permit one to study genetic and environmental influences on [phenotypes]… as well as the genetic and environmental influence on relationships among phenotypes" (Pashler & Wixted, 2002). Schmidt, et al., (2005), may have come close in the eventual outcome of selection on phenotypic plasticity. It was determined that *Drosophila melanogaster* expressed diapause (suspended development periods in an insect/invertebrate/mammal embryo due to environmental conditions that are unfavorable for development – per Dictonary.com) phenotypes that were highly variable, and that variation was reflective of the population's latitudinal location when they were collected from the wild. 750 lines were collected and studied to determine each population's diapause phenotype, starvation resistance, and fecundity. Crosses with non-diapause expressing lines showed in all but one case the offspring of the crosses all expressed the parental diapause phenotype- indicating diapause is a dominate phenotype. And while the incidence of expression was shown to increase with latitude (the colder the environment of collection, the higher rates of expression), this is determined to be the population's evolutionary history, as the environment of colder seasons selecting on the diapause alleles to be expressed more than those in warmer climates. While crosses occurred, they were only on specific diapause populations and a non-diapause inbred line. And no testing for environmental expression of plasticity on the offspring occurred, it would be interesting to determine if diapause expression changed from the colder (more expressive line) if they were introduced to a warmer climate. Additionally crosses between two different populations under both warm and cold climates might have shown plasticity. The only conclusion is phenotypic adaptation, and phenotypic adaptation is shaped by molecular genetic mechanisms such as changes in gene expression and

changes in gene coding (Glanzman, 2010; Hofmann, et al., 2009; Schmidt, et al., 2005). These molecular genetic mechanisms of adaptation can shape genotypes (and phenotypes), such as sensory adaptations due to key gene coding changes (Dupuis, et al., 2012; Hofmann, et al., 2009; Laughlin, 1989).

2.3. Economics & utility.

A unique branch of animal behavior is the descriptive theories surrounding human financial markets and the corresponding human decision-making within those markets. While these economic decisions can be used to describe costs in any animal, most of the published work is on human interactions (Behrens, et al., 2007; de Bondt & Thaler, 1994; Dosi & Nelson, 1994; Levitt & List, 2007; Marshall, et al., 2013; Milinski, 2014). These markets can be complex, and involve layers of decisions on the individual and corporate level. The distinct problem with explaining finance is to explain the optimal choice that should be taken, and the realistic choice that must be explained after (de Bondt & Thaler, 1994).

The optimal decision making theory (or neoclassical theory of rational decision making) (de Bondt & Thaler, 1994; Dosi & Nelson, 1994; Milinski, 2014), assumes that humans are rational under all circumstances and because they are rational, humans will make rational choices, and those rational choices will be optimized because of both rational behavior, and to benefit overall well-being of the human. Optimal choice and rational decision making is theorized but not observed; assumptions made by human forecasters are false, and the model of this theory lacks the ability to quantify the

components of economic behavior (de Bondt & Thaler, 1994). This is explained in greater detail later in the chapter.

2.3.1. Evolutionary economics.

The use of evolutionary theory to mediate economics following psychology and sociology models (Dosi & Nelson, 1994) is the pioneering idea of economic curves, and economic models as they relate to human behavior and the economic markets. The term *Evolutionary* (as explained in Dosi & Nelson, 1994) is the theories/models/arguments that 1) describe how something arrived at a specified moment in time, why the something exists in its current form, or to explain the something as it moves through time, 2) the first parts explanations include random incremental units, how those units interact and combine to renew/generate a range on one variable (multiple variables can have their own ranges); the mechanisms that produced the ranges must also be included (Dosi & Nelson, 1994). In the economic world the four basic components of evolutionary theory are; i) the smallest unit that can be acted upon by the selection, ii) the construction of a signal entity from those units, and the mechanism to get from those two parts, iii) how the entity interacts with selection dynamics in some capacity, iv) detailing how a combined set of entities would generate variations among combinations of units. As this is very technical to remove the biology and any animal development from the explanation, adding back some biological terms clears up the technical confusion: i)smallest possible unit by which evolution can act upon (genes/DNA), ii) the combined units that are a set structure (genotype of a being w/out any variability) that can produce variations among the individuals in a population (phenotypes), which both can undergo environmental

selection iii) the interaction of individuals with their environments, the selective pressures, and the transformative mechanism by which the selective pressure causes the yielding of a population, and iv) the detailed condensing mechanism of selection that produces multiple phenotypes of single genes, as well as altering genes within a population. Now these can be used to construct evolutionary economic models with some slight alterations (Dosi & Nelson, 1994). So economists, having observed physical scientist using experimental modeling to understand the laws of the natural world, they assumed that these models could be used to explain and predict economies. Thus Experimental Economics (List & Levitt, 2005).

The distinct problem with explaining finance is to explain the optimal choice- touched on above- that should be taken, and the realistic choice that must be explained after (de Bondt & Thaler, 1994).

In economics there is no one simple unit of selection, though under different domains a specific unit could be named, but in general a "Fundamental unit" is a placeholder until that point arises. Fitness will also depend on the domain it is presented in, and would be judged on conflicting criteria dependent on the decision-maker, and most of the 4 F's of evolutionary biology (fighting, fleeing, feeding, and... reproduction) do not apply to financial markets. The processes how agents/populations adapt/learn and novel agents still retained, for economics can be represented in the decisions and actions of either or both individuals and organizational entities. Dosi & Nelson (1994) extrapolate this section into their fundamental hypothesis that the agents are not always rational actors in economics, and that the agents will follow context-specific rule-guided behaviors that will probably not deviate due to small changes in the economic

environment, however the agents are not static in mostly constant economic environments and will alter their choice behaviors to experiment in known environments to observe novel events, or discover novel behaviors (Dosi & Nelson, 1994). This is further broken down into the key influences of economic behavior: 1) monetary calculations, 2) how an individual's actions are both scrutinized, and to what extent the individual is scrutinized by others, 3) the "context and process by which a decision is embedded, and 4) Self-selection of the individuals making the decisions". The fourth component is a key flaw that I enthusiastically encourage can be altered to prevent observer bias (List & Levitt, 2005).

This hypothesis deviates from the standard neoclassical theory of rational (optimal) decision making for maximization of optimal responses, though the system accounts for errors in the actor/agent's behavior due to limited information are modeled into the theory, but error due to misinformation, or no information is not accounted for. Evolutionary theorist have largely abandoned a similar theory of rational acting/behavior (except as a teaching aid in classrooms) in biology, and economic evolution is reasonably abandoning the Neoclassical theory as well because of its shortcomings in being able to accurately describe the evolutionary environment of the real world. And static theories (such as the neoclassical theory) do not account for a non-static behaviors, environments, and biases, let along learned behaviors, novel choices, and competition between choice actors. A theory that can assess these and other novel effects to the system can more accurately describe the mechanisms that are occurring within it (Bullock, 1997; Dosi & Nelson, 1994; Shettleworth, 2010).

2.3.2. Behavioral economics.

Economic decision making is the maximizing of utility (not fitness), where utility is subjective to the individual and life history events (Bullock, 1997; Glimcher & Rustichini, 2004; Sanfey, et al., 2006; Shettleworth, 2010). Simple decision rules of thumb, that are naturally fit, but do not optimize utility (Chen, Lakshminarayanan, & Santos, 2006; Padoa-Schioppa, Jandolo & Visalbergh, 2006; Todd & Gigerenzer, 2007) can be rejected for a more optimal utility; this utility is quantified in a subjective, and sometimes individual, basis. Choice in utility is transitive to fitness, and this utility signal (example Signal A), is always preferred no matter which other signals are present or introduced (Shettleworth, 2010). The Optimal fitness choice may also not be chosen when offered due to these extreme situational, and individual, life history events. These economic principles were applied to predict optimal environment to produce maximal animal choice behaviors. Thus behavioral ecology (Milinski, 2014).

Levitt & List (2007) hypothesize that human decisions in economic matters are influenced by the standard monetary decisions, but also by; 1) if a subjects actions are being overtly observed, and the outward signals of emotion the observer is displaying about the actions, 2) how the action performed by the subject was activated, and why the behavior was expressed, and 3) 'self-selection of the individuals making decisions'. The model explanation begins with an elaboration that this is not an explicit model, but a simplified framework to generalize lab experiments in the paper. It then starts in on the math. When an individual has a single action choice, the effects of the individual's wealth and the moral cost or benefit will reflect upon the action choices. The moral cost/benefit have many distinct factors that could influence the utility of the action across internal

perceptions, to external, cultural cues. In this paper the moral determinates focused on will be; 1) financial externality of the choice on other individuals, 2) the set norms of the society, which may include governmental laws as they apply to the individual's society or the society that the choice is being made in, 3) and increase of the scrutiny of the action increases the moral concerns, or the way the decision making process was performed and conducted for others. "The decisions that we make are guided by the outcomes of similar decisions made in the past. Understanding how we build such associations between events, and therefore between actions and their outcomes, has been the principal goal of learning theory. According to models of reinforcement learning, when an animal receives new information, it updates its belief about the environment in proportion to its prediction error, d, which is the difference between the expected and actual outcomes. It is often overlooked, however, that d must be multiplied by an additional factor called the learning rate, to determine the degree by which the action value is updated." (Behrens, et al., 2007)

de Bont & Thaler (1994) offers some specific behavioral concepts important to economic decision making.: 1) Overconfidence; example, people overestimate the reliability of their own knowledge ("when people say that they are 90% sure that an event will happen/a statement is true, that person may only be correct 70% of the time") while depreciating other's knowledge, even if the experience of another may be more valuable. 2) Non- Bayesian rules; humans do not predict or forecast in any Bayesian form of decision making: instead Kahneman & Tversky (as described in de Bondt & Thaler, 1994) outline that people produce their own probability judgements based on "representative heuristic." This Heuristic is how people calculate the probabilities of

uncertain events; “by the degree to which it is : i) similar in essential properties to its parent population; and ii) reflects the salient features of the process by which it is generated”. This model has shortcomings in inducing the Observer-expectancy effect (a.k.a. Hawthorn effect; Observer effect- The primary flaw in typical lab experiments is the Hawthorn Effect (observational effect), as the observed experimental subjects would not face the level of scrutiny in real economic markets so (in this paper) it is more likely the lab experiments were influenced towards moral cost/benefit concerns over wealth due to the theorized scrutiny affecting moral factors not wealth ones (Levitt & List 2007) on the subjects to weight recent observations above collective past prior odds (despite the past odds is collectively determined by many observed events). These people would also forecast to the outliers rather than average their probabilities. 3) Loss aversion, framing & Mental Accounting; describing Markowitz use of semi-variance as a measure of risk, which helped develop Kahneman & Tversky’s theory of decision-making under uncertainty, or Prospect theory. Losses (or negative changes in wealth) are weighted double to any gains. Loss aversion is a step further, using the description of action choices (framed) to implicate the sensitivity of decision-making. (“For example, a store that offers cash customers a discount is less likely to upset its credit card clientele than another store- with the same prices after these events- that imposes a credit card surcharge.”) When individuals create their own frames of actions in decision making, it is mental accounting. 4) Fashion and fads; people are influenced by others; a simplified way of thinking of sociology and social phycology. 5) Regret, responsibility, and prudence; Regret is only the remorse of any decision that lead to a bad/undesirable outcome. The remorse can influences decision-makers to preform additional actions to avoid regret

entirely. Dr. Richard Thaler (1985) explained mental accounting as three behavioral variables that translate to the "Transaction Utility" which can be evaluated mathematically. The value function which is indicative to each individual- in this case humans- which is defined by Thaler as v (·). This value function can be affected by psychophysics of quantity, and can be influenced by an "endowment effect" when the loss factor is at a greater slope than the gain function.

These economic values of cost and utility will be used under the context of choice selections, and investments in behavior. In order to understand the cost and utility of behavior a closer look at sensory systems, signal detection, and biases needs to be analyzed.

3.0. Sensory Systems & Signal Detection Theory

Sensory systems are complex mainframes of receptors that react under different environmental signals to stimulate a receptor system that is passed along to a higher processing unit to elicit a response (Stevens, 2013). In biofilms or fungi systems, outer (external) layer cells sense changes in the environment and transmit via intercellular signaling to internal (protected) cells. These internal cells react to this signal and produce chemicals required to improve the overall survival of the complex system. In most vertebrates these internal signals are processed in the brain. The brain then interprets the signal into a reference for reaction. This interpretation can recall past experiences, knowledge, and conditioning to show a bias in the response (Ney-Nifle, Keasar & Shmida, 2001; Shettleworth, 2010), or a desired behavioral outcome (Stevens, 2013). Some general sensory systems are;

1) Chemical (or chemo-sensory systems); since chemicals are discrete, compact, and limited by structure, these signals are non-continuous; and they can be disrupted by special distributions and environmental dispersion events. An example of a specific chemo-sensory system is Olfaction and the corresponding odors associated with that system. Once the odor (the chemical signal) is detected using the specialized receptors that are attached to, and diffuse, the molecules into the lymph fluids and to the olfactory receptor neurons, the olfaction system is activated. This detection is then used for orientation and localization of the signaler due to the odor disruptions. Chemical sensory systems are unique in that orientation towards the signaler is needed.

2) Light detecting sensory systems have different levels where detection of the electromagnetic spectrum is increasing with complexity. In phototaxis the orientation towards/away a light source is sensing light, but no vision is required. Adding a photoreceptor, a specialized wavelength receptor that can be specialized to specific wavelengths of light, creates the situation where vision develops. This vision is limited to a described monotone world- however this monotone is not black and white, and can be further explained later in the chapter. Color vision can develop from two or more of these photoreceptors with different spectral sensitivities within a single visual system of an individual.

3) Mechanical system(s); though only described under sound vibration detection. Though visual detection of vibrations is a quality of this sensory model, it is an understudied system. Additionally, echolocation sensory systems/organs are unique in that mechanical sound is used to determine the environment, this is done by the mind, not by visual organs. In general communication/speech research in sound detection is the most studied

of the mechanical systems. The signal waves are detected through a space/medium, which are categorized by velocity, frequency, intensity, and other significant representations (Stevens, 2013).

Sensory systems are tasked with primarily detecting and discriminating signals from background noise and reacting accordingly to the signal (Nilsson & Warrant, 1999; Stevens, 2013). The goal of the sensory system, or the receiver, is to optimize their ability to correctly identify a signal from background noise, and responding to the detected signal; this is known as Signal Detection Theory (SDT). Abdi (2007) explains this theory using a face recognition example; if a face had been seen by the recipient before, they had to answer if they had (yes response) or never had (no response) seen the face before. Each of these answers then has to be analyzed on accuracy- if a face was recognized correctly I would be called a hit, but if the responder answered "yes" to a face they had not seen before, that would be a false alarm; See Figure 1. Additionally if a face was designated as having not been seen before ("no") and that answer was correct then that response would be a "Correct rejection", alternatively a face that was designated incorrectly by the receiver as not having been seen before (but they had seen it) is a "miss".

The SDT model expands on the above example to analyze the response systems that an individual can take, using intensity of a hidden variable and the responses of the participant (Abdi, 2007; Akre & Johnsen, 2014; Allemand & Bouletreau-Merle, 1989; Bullock, 1997; Goldsmith, 1990; Milinski, 2014; Osorio & Vorobyev, 2008; Pashler & Wixted, 2002; Rushton, 1972; Stevens, 2013; Vorobyev & Osorio, 1998; Vorobyev, et al., 2001).

A system of processing signals can get complicated based on what information is valued, which sensory system is preferred, and how that information is obtained (Stevens, 2013) such as biases for the use of vision over sound senses, and how those signals were detected. Energetic tradeoffs for the maintaining and receiving of signals, and the energy cost to process the signal, can be inefficient if the signal is interpreted incorrectly, or if the signal is missed (Taylor, Gilbert, & Reader, 2013). For example, in a vision system to increase the size (surface area) of the eye would collect more light waves, and gain more information on general areas, but as the opening increases in size the details become blurry without the corresponding increase in photoreceptors. Additionally more receptors cost more energy to make and maintain than fewer, but fewer receptors cannot process or detect as many light signals (Stevens, 2013). Tradeoff for larger photoreceptors to collect more light, but this is a cost of quantity of photoreceptors to resolve an image (Nilsson, 2009; Stevens, 2013; van Hatteren, 1992). In the case of flight patterns in flies in low light environments, fast flying species had a higher rate of phototransduction mechanisms, and the reverse is also true (Chittka & Menzel, 1992; Gomez & Thery, 2007; Holopainen, 2008; Kevan, 1972; Laughlin & Weckstrom, 1993; Liu, et al., 2006; Masland, 2005; Stevens, 2013; Weckstrom, Hardie, & Laughlin, 1991).

Adding another layer of complexity in sensory systems is the processing and interpreting information in tandem. This is the ability to use two or more sensory systems (and the multiple signals the systems can interpret), to gain a more robust conclusion of the combined information (Guo & Guo, 2005). This conclusion also narrows down behavior, and information that may be lacking in the observation. This is not always an additive processes, as sometimes the information processed by the different sensory

systems can conclude different, and sometimes, contradictory information. Under those unique circumstances, which signal (and signal system) should take preference? If there is a preference of System A over System X, is there an intensity of Signal X that would cause System X to be preferred over System A (Stevens, 2013)? As an example; in a surprise system, an expected signal of the environment moving is interpreted to mean the resulted signal is an earthquake, but if the furniture is moving without the additional movement of the walls/floor, then another conclusion should be reached, but usually is this not the case. The furniture moving is more easily discernable to the human eye than the walls of a shelter moving that they are inside of. This is a weighted cost and a visual bias of the signal information (Holopainen, 2008; Mayr, 1988; Raguso & Willis, 2002; Stevens, 2013).

3.1. Bias.

The combination of how information from the environment is sensed, and how that information is used by an individual is Sensory Bias. This sensory bias is completely dependent on genetic history and life history events. At some point during the evolutionary history an innate preference for one sensory system over the others, or one component of a sense over the others (Arak & Enquist, 1993; Bullock, 1997; Greenfield, 2014; Lunau & Maier, 1995; Lunau, 2014; Mery & Kawecki, 2004a). After the innate preference has occurred, further life history events (such as pain relation or Pavlovian conditioning (Shettleworth, 2010)) cause a preference or bias directed at a stimulus that either there was no previous cause for bias, or there was a positive preference that was conditioned against. As an example: in the case of brood parasites in cuckoos, if a female

bird is on her first clutch of eggs and the first hatchling to emerge is the cuckoo, then that female is forever conditioned to recognize cuckoo hatchlings as her own, which is a negative bias she has developed because of her life experiences (Goulson, et al., 2007; Gumbert, 2000; Shettleworth, 2010).

The broadest definition of a bias is any active or passive prejudice that can cause a deviation in an individual's behavior compared to the standard (non-biased) population. However a non-biased population may not exist in nature. Endler (1992) describes the events that create biases as "sensory drives" towards evolution, with sensory systems and their conditions being the force of evolution. It can be implied that biases should be observed within the context of sensory systems and some functional processes of biases will be discussed within the context of Sensory Ecology later. However a brief explanation of some evolutionary models of bias development are discussed below.

Endler & Basolo, (1998) lists the types of biases as; "1) biases resulting from properties that once had a particular function that is now lost, 2) biases that are incidental and even non-functional consequences of how organisms are built, 3) biases that have a function outside the context of sexual communication, 4) biases that have a function in sexual communication but are so fundamental to the sensory system or brain they bias further evolution, and 5) biases that has no previous function but were established by mutation and not selected against. The discussed models above emphasize different combinations of these biases; Sensory Drives, Sensory Exploitation, and Perceptual Bias discuss all five, Sensory trap elaborates on number 3, and sometimes 4. Hidden Preference stays with number 2, Receiver Psychology/Perceptual Drive models emphasize 2, 3, & 4. And since all but number 4 document evolution of preferences

without male signal and it heritability, as these biases can be produced though evolution by other means that are not sexual communication.

3.1.1. Sexual selection.

Perception of conspecifics, or of unique characteristics can elicit a sexual preference, or sexual signal bias, for the unique signal. Specifically, and generally, a perceptual bias in females is determined by unique behaviors or signal systems of the male. These unique male developmental characters were described by Darwin (1871) as inherently conspicuous, unique, and in direct opposition of natural selection (Shettleworth, 2010). These perceptual biases are often explained by colorful bird plumages, showy behaviors, or both acting together. Endler & Basolo (1998) and Ryan & Cummings (2013) do an exceptional job explaining the many selective models that could create a perceptual bias (PB), focusing on the sexual selection scenarios by which those can arise. Mate choice (MC) can be assessed under sexually selective pressures, and non-sexually selective pressures (Alonzo, 2009; Leadbeater & Chittka, 2007; Milinski, 2014; Naisbit, Jiggins & Mallet, 2001; Shettleworth, 2010).

Initially the signal that communicates the unique characteristic is constrained by the sensory system of the receiver, and how that receiver can processes, extract, and asses the signal. For Mate Choice (MC) the acting upon the signal is an additional requirement. The evolution of the signal to be more conspicuous, and be more receptive to the sensory system, is biased towards the receiver's ability to process the signal (Niesenbaum, Patselas & Weiner, 1999; Oberrath & Bohning-Gaese, 1999). And while the signal can also be affected by environmental and biophysical constraints, the emphasis on sensory

systems and the ability of the signal to even be detected is the focus on this sexual selection model known as sensory drive (SD). SD is used by Endler & Basolo (1998) as a model that will be translated into other sexual selection models, and Boughman (2002) defines sensory drive as "the integrated evolution of communication signals, perceptual systems and communication behavior because of the physics of signal production and transmission, and the neurobiology of perception". With sensory drive, the first rule is that perceptual biases are not static, as populations have natural variations within sensory systems, and signaling capabilities. Since the environment can also cause evolutionary changes within the neural networks of sensory systems, the directional evolutionary biases would perpetuate the evolution of signals that are louder, more readily processed, and conspicuous (Boughman, 2002; Endler, 1992; Endler & Basolo, 1998; Renoult, Kelber & Schaefer, 2015). Though this is not the only direction.

The emphasis of the sensory systems directing signal evolution is the receiver bias models, which have three described categories of initially non-sexual selective systems of evolution (Rodd, et al., 2002). First is pre-existing bias (PEB) where a distinct bias for a trait is due to some other selective force before it is selected upon by sexual selection. Also called the "runaway" hypothesis of sexual selection (Chittka & Menzel, 1992; Seehausen, et al., 2008; Shettleworth, 2010). These male traits could have arisen by genetic drift and the sensory (or cognitive) system processing the trait signals is biased for those different trait qualities. In Endler & Basolo (1998), Basolo lists qualities a male trait needs to have to be classified as PEB, which are specific to the trait being present, the trait is used in mate choice, the trait evolved from an ancestral species that did not have the trait (or the trait existed in a non-modern form), the preference for the modern

trait evolved before the specialization of the trait, and that the bias present can be used to determine the further direction of evolution. Though these qualities are oddly specific they are distinct from the sensory exploitation (SE) model (Endler & Basolo, 1998).

The SE model focuses on sensory drive's ability of a sensory system to detect a signal. The properties of a sensory system to detect/process a signal can vary within and between species. Not all signals stimulate the system in the same way, and so the traits that produce a signal that causes successful stimulation of the sensory system is preferred by the female. This could be as simple as the signal being distinct from background noises, and the sensory system being uniquely adapted to detect the signal (Chiao, et al., 2000; Endler & Basolo, 1998; Wakakuwa, et al., 2010).

The last of the described receiver bias models is the sensory trap (ST) model. Which focuses on the neural responses to the signal once it has been received. This could be behavioral output response, or it could be a cognitive association. An example could be a behavior that creates fitness benefits that are unique, or neural stimulations that create peaceful and non-costly emotions in the receiver (Endler & Basolo, 1998).

Hidden preference (HP) models focus on neural networks, their genetic coding, and the link to learning and discrimination with the sense organs being experimented on. These hidden preferences can be represented in any from, but can be tested and trained on, which can result in similar signals being detected. These learning /discrimination/ training experiments must first test if a hidden preference exists when a novel signal is introduced. If the testing shows a hidden preference related signals to the novel tested could also be discriminated against. If the novel signal uncovered a hidden preference, other hidden preferences could arise under distinct novel signals. And even two novel

signals that produced differing hidden behavioral responses could create a divergent point of selection for trait preferences. Though oversimplified for a liner evolution system, it is a model of preference (Arak & Enquist, 1993; Endler & Basolo, 1998; Ryan & Cummings, 2013).

In a more complex case (which can be described within the context of hidden preferences); receiver psychology and perceptual drive (RP/PD) models directly uses sexual selection as the driving force of evolution. In RP/PD novel stimuli are favored under habituation/elaboration systems, and complexity of a signal is favored for its additive effects on behavioral responses. A return to the optimal recognition system, however these "perfect" systems would never evolve, as it is statistically improbably that a sensory system to have experienced every possible stimuli variation within the species life history. There are innumerable stimuli to one sensory system, and since selective scenarios use behavioral responses to a small number of stimuli, using the evolved system, or the behavior, as a predictive system to how an animal will behave under novel stimuli is unfounded (Arak & Enquist, 1993). Peak shifts and supernormal stimuli use RP/PD models (Endler & Basolo, 1998; Ryan & Cummings, 2013).

3.1.2. Supernormal stimuli & peak shift displacement.

In the case of testing evolutionary behavior in a laboratory setting, the use of artificial or exaggerated stimuli can cause the evolved behavior to be expressed more strongly, or to be expressed in a more efficient way (Barrett, 2010; Rowland, 1989; Tinbergen, 1963). This extreme behavior can cause a preference for the artificial stimuli over the natural stimuli without training (Shettleworth, 2010). This hijacking of the

normal response/ behavior has been shown in repeated experiments (Baerends, 1982; Hailman, 1967; Staddon, 1975; Tinbergen, 1951; 59; 63). It is hypothesized that this behavior manifests because instincts and behavior have no bounding, or limit in space-time, represented in nature, and the more general a preferred stimulus is when evolved, the greater range the stimulus can take to elicit the same response (Arak & Enquist, 1993; Barrett, 2010; de Bluck & du Laing, 2010; McMillen, 2011; Staddon, 1975).

These unique reactions were first documented by Tinbergen & Perdeck (1950) many other hypothesis have emerged and fall into two rough categories of 1) Learning-effect hypothesis, or 2) Innate- bias hypothesis (de Bluck & du Laing, 2010). The major study of learning- effect is the Peak Shift model (Staddon, 1975); where it is assumed, and has been documented, that the individuals in a population are rewarded for signal detection on one end of a scale, and punished for reaction to the stimulus from the opposite end. In the adaptive gain/loss tradeoff (Frankino, et al., 2005). Darwin explained how energy used in one action (behavior, etc.), is energy that cannot be used in another action, such as energy being used to hunt for food is energy that must be taken away from mating behavior, or parental care.

Innate- bias hypotheses is used to explain the supernormal reaction as an adaptive or exploitive recognition system bias (de Bluck & du Laing, 2010). Arak & Enquist (1993) modeled a neural network to test the hypothesis that if perpetual biases exist in sensory networks, then the selection pressure would be on the signal, not the receiver. This hypothesis has two mainstays: 1) no perfect recognition system can be evolved in nature, because 2) there is a nearly infinite number of forms a stimulus can take, so a receiver cannot have evolved under all possible variations of the stimulus. So the receiver

is evolving under a small number of stimuli, an asymmetric selection pressure, and natural variation. This would then allow for coevolution of the signal and receiver because Arak & Enquist assume that 1) signals always become more exaggerated past what the receiver needs to activate, 2) #1 occurs at a cost to the signaler, 3) as the signal continues to be exaggerated the receiver will lose responsiveness to it, and 4) selection favors signals that become increasingly exaggerated, to prevent eavesdropping.

de Bluck & du Laing's (2010) paper reviewed other Innate-bias experiments (including Arak & Enquist's which was criticized for their neural networking model, but it resembled a later study's results). Non- functional biases have neutral, non-selective bias, which would arise under Arak & Enquist's hypothesis.

Then there are functional biases; the use of receptors as multi-dimensional activation sites for the signal to rearrange itself on. For instance a receptor can sense a signal's shape, color, intensity, size, etc. Each description is a dimension of variation that a signal can take, each separate dimension of the signal is activated separately on the receptor (at differing levels), and each dimension's receptor must communicate together, where miscommunication can occur (de Bluck & du Laing, 2010).

Lahti (2015) discusses the limits of artificial stimuli in behavioral experiments, noting his own undergraduate failures, but also describing the main pitfalls of the key types of experiments, and acknowledging that artificial stimuli still can be used. In the case of supernormal stimuli experiments the failure occurs when the design 1) varies more than one feature of the stimuli without a control, and/or 2) exaggerates the stimuli to the point that the supernormal stimuli is considered a novel stimuli to the subject. In

the case of the first if a study uses wood eggs for supernormal stimuli, but the 'controls' are painted white- this is two trials.

Under selective conditions to a population, when two stimuli are used as ranges of one sense (or variations of a stimuli), the experiment conducts a condition asymmetry to occur. Assuming this example is color vision, and the two stimuli are two wavelengths on opposite sides of a spectrum (e.g. 440 nm and 600 nm). Assuming the animal being trained can see both wavelengths, and in general the peak sensitivity is somewhere between the two stimuli, then an experiment where the lower wavelength is selected against, and the higher is rewarded, an asymmetric conditioning experiment is occurring. In this case the animal is rewarded if it responds to the higher wavelength, and punished if it responds to the lower wavelength. This would cause the peak sensitivity to shift towards the higher wavelengths, which would create a selective pressure (Staddon, 1975). While this type of experiment does not exclude the development of supernormal stimuli, the constraints on visual color perception could prevent supernormal stimuli from occurring in this specified example.

3.1.3. Weber's Law.

The comparison of signals in decision making is not valued in a straight, simple, linear slope, where the exact differences between the stimuli are the perceived differences. Sensory systems, and nature, are not so simple. Weber's law postulates that the perceptual comparisons are made on a proportional magnitude scale- Proportional processing. As an example in female mate choice a just noticeable difference (JND) between traits is the threshold by which a difference can be perceived between the traits.

In chase-away selection the JND of these sexually selected traits increases due to costs incurred by a female when mating with males that have exaggerated traits. As if the females are habituating to the signal that stimulated her behavior in the past, the JND required to elicit the same level of behavior needs to also increase in orders of magnitude. Of course these "habituation" and female costs for selection do not occur within one individual, this is predicted to be her daughter's and future granddaughter's bias, and JND thresholds that are shifting the sexually selected trait towards more loud, more intense, more conspicuousness stimuli (Akre & Johnsen, 2014; Ryan & Cummings, 2013; Shettleworth, 2010; van Hatteren, 1992).

3.2. Sensory ecology.

In the broadest definition Sensory Ecology is the study of how sensory systems developed, the components of the system, and how the sensory system(s) are used by the organism for behavioral or evolutionary purposes (Alcock, 2009; Davis, Krebs & West, 2012; Dawkins, 1976; Endler, 1992; Raine & Chittka, 2007; Stevens, 2013; Vosshall, 2000). Barlow (1982) describes all sensory systems as having some basic properties in common despite how unique the systems are: all systems share instruments/organs that detect specialized physical energies (Shettleworth, 2010; van Hatteren, 1992). Chittka & Briscoe (2001) explains that in order for sensory ecology studies to explain evolution phylogenetic analysis, molecular studies, variance of these systems between individuals, considerations of pleotropic effects, biogeography, consideration of random evolutionary effects, fitness tests, and selection experiments need to be included; though hardly any experiments will have all of these components in one paper.

Not all sensory systems are created equal, nor are they equally sensitive to detect small changes in the signal cues. Quality of the stimuli is important to exciting the sensory organs, which includes intensity, loudness, sweetness, and/or brightness. These qualities affect if a difference between two stimuli can be sensed by the sensory system. This Just Noticeable Difference (JND) threshold is Weber's Law described above (Akre & Johnsen, 2014; Henze, et al., 2012; Shettleworth, 2010). Specialized sensory systems are used to obtain information from the environment, but there is no absolute threshold of response to stimuli, as an extreme 'no-behavior verses behavior' thresholds do not exist in nature; this can be simplified, since there is a limited amount of stimuli a sensory system has experienced in evolutionary history and there are a near infinite number of ranges a stimuli can take, the limitations we would predict to occur due to threshold constraints, prevent absolute predictive value with novel stimuli- you can never know how an animal will behave in response to a novel stimuli until an experiment is conducted to determine the behavior response.

When an individual is observed in nature, how an animal behaves and reacts to its environment is a representation of its evolutionary history. However, the systems that the individual relies on to sense and obtain information about the environment is also indicative of its evolutionary history, especially if some of the sensory systems have become vestigial, or if a new niche-sense has been obtained. A butterfly that possesses an extra color vision receptor can see UV light and process that information into cues for nectar or egg laying sites, depending on what that UV signal indicates, which influences how that butterfly will use that information (Cuthill, et al., 2000; Lewis, 1989; McNeely & Singer, 2001; Pashler & Wixted, 2002; Ruiz-Dubreuil, Burnet & Connolly, 1994;

Shettleworth, 2010; Song, et al., 2012; Waser & Price, 1981; Weiss, 1991, 1995, 1997; Weiss & Papaj, 2003). This novel UV sensor is specialized to detect energies humans cannot within senses humans have developed. There are sensory systems that have been developed that humans do not have, such as echolocation and magnetic fields (Manger & Pettigrew, 1995; Shettleworth, 2010; Wiltschko & Wiltschko, 2006). These systems are used to detect patterns, find mates, forage for food, discriminate within and between signals, and process social information (Alonzo, 2009; Althoff, Segraves, & Johnson, 2014; Anderson & Dobson, 2003; Bradbury & Vehrencamp, 1998; Bullock, 1997; Clark & Evans, 1954; Collett & Collett, 2002; Endler, 1992; Endler & Basolo, 1998; Endler & Mielke, 2005; Endler, et al., 2005; Fleishman, Leal & Sheehan, 2006; Frederiksen, Wcislo & Warrant, 2008; Ghazanfar & Santos, 2004; Ryan & Cummings, 2005; Shettleworth, 2010). Determining the perception of an animal is analyzed by the psychophysics of the animal in relation to the signal being perceived (Shettleworth, 2010). These signals can be tested through 1) electrophysiology, 2) natural behavior changes in varying simulations, and 3) learned behavior testing. Shettleworth (2010) describes how the first test can determine is a cue/stimuli/signal can be sensed. The second is harder to apply to all the ranges the old stimuli can excite behavior, and the third is determined by laboratory studies. The third is also cautioned to be hard to replicate in the wild, especially if the subjects of learned behavior required training before discrimination or learning could occur, but this is not an absolute law.

In animal behavior, it has been documented that psychophysical trials follow three principles: 1) stimuli that are more intense tend to cause sensory neurons to respond as physically more intense, 2) sensory systems habituate to unchanged stimulus, and 3)

response to stimuli is determined by the contrast to background noise (Maynard Smith & Harper, 2003; Mayr, 1954; 1963; 1982b; Platt, 1964; Ryan & Cummings, 2005; Shettleworth, 2010; Stevens, 2013).

Referencing back to evolutionary economics and behavioral economics, the ability to obtain information in sensory ecology is to take on a cost to obtain the information, and processes it to gain better utility, and in biology, an advantage (usually in learning). And since an individual is interacting with individuals within its own species/population, and with individuals from other species, changing environmental information should be obtained in an "optimal manor". The cognitive mechanisms (perception and memory) uses this environmental information to result in optimal behavior (Shettleworth, 2010).

Costs in information gain, and cognitive mechanisms, will be classified as the energy expended to perform the behavior, with the expected end result of the behavior to obtain more energy than was used. Further costs can be quantified depending on information gathering systems and models. Uncertainty in the environment can pose fitness problems for an animals, so to reduce uncertainty information is gathered (if it can be) (Dall, et al., 2005; Keaser, et al., 2006; Lunau & Maier, 1995; Nuzhnova & Vasilevskaya, 2013; Partida, Rubalcava & Alarcon, 2010; Raine & Chittka, 2007).

There is a cost to this information gathering (Mery & Kawecki, 2004a), energy and time usually spent on other tasks are re-allocated for information gathering. There are direct interactions with the environment (personal information), as opposed to the observation- and analysis- of other animal's behavior within the environment (socially acquired information).

In marginal value theory (Shettleworth, 2010) the patch foraging of a predator for prey/food (birds and seeds were used as an example) has costs expended if the patch is constant; the predator finds and eats the prey, so the energy lost to gain the prey is maximized for optimal utility. This simplified static environment has its additional costs of time spend hunting prey which could be time not spent mating, or finding shelter, or looking for predators that are going to eat you. However, in most patches the available prey/food depletes over time. So the predator now has to assess when the current patch is too depleted to continue foraging, and find a new patch. The act of finding a new patch now quantifies additional costs; time spent looking for a new patch is now time not foraging for food- which may already be time away from other behaviors. Costs of finding a patch that is more depleted than the one left behind, additional travel costs to return to a shelter from the new patch, competition for the prey by other predators that consume the same prey, and predators could be hunting you during the time finding a new patch, and may be waiting at the new patch. These costs are compared to the costs of remaining in the original depleted patch, which contains the same costs as the static patch, but now the costs of staying as the food depletes, more energy expended for less prey gained, and if a home shelter is not nearby, lack of energy to return home is a possibility (Goulson & Cory, 1993; Goulson, et al., 2007; Gumbert, 2000; Zimmerman, 1979).

Time constraints can add further costs to the optimization systems, where the cost to reaming in an open patch after a determined amount of time (say after dark, or being a sitting duck in the same place for two hours is asking to be killed), can cause irrational behavior where quick choices on prey that are readily available but don’t give much

energy, where the assessment of anything is better than starving, and the waiting for better prey cannot guarantee that more energy-rich prey will appear within the set time constraints (Bell, 1990; Bullock, 1997; Lihoreau, Chittka, & Raine, 2010; Shettleworth, 2010).

Learning and memory in the searching of information, can reduce some of the costs to information gathering in foraging. If patches replenish over time, or if depleted patches can be remembered, then costs expended in returning to a depleted patch reduce. And a replenishing patch that has a set cycle under which it will replenish, then the ability to learn and perceive when that timing cycle passes will decrease searching costs for other patches, and prevent energy being expended when the cycle has not finished, and foraging in a depleted patch (Bell, 1990; Kuntz, et al., 2012; Shettleworth, 2010).

So learning behaviors which obtain and store (in neuronal configurations) new information this can be a) spatial environmental configurations, b) sensory information, c) associations between perceived stimuli & environmental states, or d) motor patterns (Dukas, 2008). Learning models build associations between past and future events, the learning rates, and reinforcement using new information to update current knowledge about the environment (determined by prediction error) (Behrens, et al., 2007; Heisenberg, 1995; Keaser, Motro & Shmids, 2013; Wang, et al., 2008).

Animals, using selective sign stimulus (signal bias), respond to objects in their environments (Evert, 2005; Tinbergen, 1951), where the collective whole of the signal, not the individual parts of the signal, are interpreted (Margolis, et al., 1987; Shettleworth, 2010).

3.3. Visual ecology.

As for visual ecology, the same restrictions apply to discrimination and biases. The female sexual selection of a color trait in birds has a proximate causation of the signal- intensity of color- representing a male that is best to copulate with. The ultimate causation of this behavior is the sexual selection and evolution causing the most intense colors to persist in this species. Genetic preferences can be both proximate and ultimate. The birds can receive and are biased towards the more intense color signals by having the genes necessary to interpret the colors. The visual receptors that can sense the signals and the genes that can produce those flashy signals would be classified as an ultimate causation (Alcock, 2001; Endler, 1992; Tinbergen, 1963).

In terms of female choice, the color signal that would excite, or activate, her receptors the most would be a preferred choice based on preference bias, and context (Endler, 1991; Houde, 1997). As the color signal has to travel some distance to activate the visual sensory system, there is also the chance for environmental conditions to affect the signal, such as time of day and abundance of overgrowth (Endler, 1992; Endler, 1993), where the filtered light can create a unique system where male color can me muted or enhanced by the environment. Additionally, signals have a greater risk of being intercepted and eavesdropped on (Bicker & Reichert, 1978; Brandley, Speiser & Johnsen, 2013; Osario & Vorobyev, 2008) as the greater distance is covered, and how specialized the signal is (Darwin, 1871; Endler, 1992). This is key for co-evolutionary systems. Ryan & Cummings, (2013) documents how the perceptual biases are not necessarily or often costly to the females due to direct proximate benefits that occur for the females.)

By specializing receptors and the signals in co-evolutionary systems, where the signal becomes tuned to the receptor, and the receptor more towards the signal gradually. The chances of eavesdropping decreases without the specialization of the eavesdropper also occurring, which is an evolutionary arms race to specialize the sensory systems. This in turn affects behavior (Brandt & Vorobyev, 1997; Endler, 1992; Masland, 2005).

Wavelength dependent behavior is an indicative mechanism where some colors predetermine a behavioral reaction (Lunau, 2014). For example a male displaying, causing a female to want to mate. This system, while important, is a hit or miss kind of system (Endler, 1992), because the male can either hit the desired threshold or not. This behavior is assumed to have originated with a selectively neutral bias, with a range of selective wavelengths, or the behavior would not have persisted, and died out with other more costly behaviors. Additionally, in some cases the wavelength dependent behavior is so detrimental to the individual that questions arise on how the behavior persisted, as is recorded in the case of flashy and colorful dances to attract mates, which will also attract predators (Anderson, 1994; Darwin, 1871; Maynard Smith & Harper, 2003; Millar, et al., 2006; Searcy & Nowicki, 2005; Skorupski & Chittka, 2011). This is the Sensory Bias Hypothesis (Endler & Basolo, 1998; Ryan, 1994) where runaway sexual selection of female choice began with females having preexisting preferences of these colorful indicators before the males had developed the feature, which behaviorally can be expressed in a secondary function (Fuller, Houle, & Travis, 2005; Millar, et al., 2006; Rodd, et al., 2002; Searcy & Nowicki, 2005), such as in non-sexual behaviors, where the red of a favorite fruit is the red of the male color the females prefer.

4.0. The Evolution of Eyes & Their Visual Systems

Though visual ecology jumps into describing the processing of visual information within the environment (and the behavioral systems in place to respond to unique receptions), vision is a diverse sensory system, with highly studied levels of evolution and function. In this section the specific structures and process systems that create visual systems will be combined with the known evolutionary histories and competing hypothesis.

Roughly 530 million years ago (Mya), during the Cambrian epoch, there is a significant amount of fossils that depict many versions of compound and lens-type eyes that evolved within a 5 million year window (Cronin, et al., 2014; Fernald, 2004; Fernald, 2006; Gehring, 2005; Gehring, 2014; Goldsmith, 2013; Land & Nilsson, 2012; Nat Geo Evolution, 2016; Parker, 1998; ScienceHook, 2016; TED-Ed, 2015; Yong, 2016). This explosive speciation has no defined cause, though many theories have arisen. Such as the accelerated eye evolution occurring because light emerged as a behavioral signal- a majority of fossils have groves and iridescence that would have been flashy to predators and possibly drove them away (Parker described by Fernald, 2000).And however elegant this theory is, many selective pressures could have also been occurring, and maybe none of the proposed theories reflect the accurate evolutionary selection pressure.

While there is a ton of fossil evidence of the Cambrian Explosion of eye diversification, the precursor to these eyes has little fossil evidence at all. At best the evidence is that small, soft bodied creatures left trail marks in the sea floor, indicating movement (possibly phototaxis), with the quantity of these grove routes increasing up to the Cambrian. As little is known about the exact components of the eyes in the Cambrian

(Nat Geo Evolution, 2016)- fossils only preserve (and show) so much- a back tracing of simpler and simpler systems of eyes that are still hypothetically useful to the ancestor possessing the visual organs.

In the case of visual systems, a simpler eye would evolve to support more complicated tasks without losing the less complicated underlying configuration. In this case Nilsson argues (Cronin, et al., 2014; Land & Nilsson, 2012; Nilsson & Arendt, 2008; Nilsson, 2009) that the evolution and demand of more complex visual tasks lead to the evolution of the eye. Since all eyes collect light, using a lens to focus an aperture onto specialized photoreceptors and/or photo-transducing cells, and during the Cambrian functional eyes emerged in three phyla; chordates, mollusks, and arthropods (Fernald, 2000).

Nilsson (2009) lists the increasing complexity of events of the evolution of the eye into four distinct stages: 1) A way of monitoring ambient (non-directional) light that controls wavelength dependent behaviors, 2) Directionality of light is obtained, 3) low spatial resolution allowing more complex visual tasks, and 4) high resolution vision abilities (C0nc0rdance, 2009; Cronin, et al., 2014; DonExodus2, 2008; Land & Fernald, 1992; Land & Nilsson, 2012; Nat Geo Evolution, 2016; ScienceHook, 2016; Yong, 2016); see Yong (2016) for an overview and to be consulted during this section. It is also of note that in the four stages of increasing complexity, only the first does not need opsins to preform, but every other documented case of increased complexity in stage two and higher does require an opsin (Cronin, et al., 2014; DNews, 2015; Yong, 2016). What an opsin is will be detailed later in this chapter.

Then stepwise evolutionary abilities, from opsins, to visual pigment sensors, to photoreceptors, to the visual organ (the eye), and beyond. Though mathematical representations of the complexity of cognitive models has not been quantified or productive (Chittka, et al., 2012).

4.1. Circadian clocks & proto-eyes.

Internal timing systems that are developed by cellular oscillations, and synchronized to some environmental cycle (usually a day-night 24 hour cycle), and this mechanism is perpetuated in virtually all organisms that have been tested (Gehring, 2014; iBiology, 2014a; Peirson, Halford & Foster, 2009). However these 'transcriptional-translational feedback loop' (TTFL) synchronized systems are not conserved across these taxa; the proteins and genes involved with the circadian oscillations are different in quantity and type, three proteins are involved with cyanobacteria, and animal clocks use only two transcription factors that are very different from the cyanobacteria, and the fungus and plant clockworks use two transcription factors too, but those proteins are different between each other, and distinct from animals and cyanobacteria (Loudon, 2012; Ribelayga, Cao, & Mangel, 2008; Vinayak, et al., 2013). This would imply an independently evolved emergence, however studies in red blood cells (O'Neill & Reddy, 2011 as described by Loudon, 2012) determined a second oscillation system in the oxidation state of peroxiredoxin (PRX) proteins that is robust. This PRX model is strongly conserved across species with red blood cells, and appears to work with the TTFL model on other PRX rhythms that appear in other organs. And since PRX

oxidation proteins are nice to have to prevent oxygen poisoning, they are found in flies, plants, fungi, and cyanobacteria (as described and tested in the paper Loudon, 2012).

Additional testing occurred to determine oscillation rhythms in the PRX model if the TTFL system was turned off. It was observed that the PRX oscillations shortened or lengthened depending on the TTFL mutant, so there is some coupling between the two circadian systems, but they are not directly tied together (Loudon 2012). Though it is assumed that the PRX system arose during the great oxidation event (GOE) 2.5 billion years ago, the two systems of circadian clocks are not connected in evolutionary history (Loudon, 2012). I would postulate, that since PRX was conserved, that the independent evolution of the TTFL systems in the other taxa was possibly due to a duplication of the genes, because having two independent clock systems that could communicate would prevent miscalculations on a cell, or organism's part, to miss anything of import.

Since these clocks are synchronized by environmental signals, which include light, but not always, this mechanism can be seen as the first evolutionary step toward vision (Gehring, 2014). Since other external factors can regulate the "biological clock's" oscillations, the mechanism's ability to also use light could be indicative of sensory system adaptation to novel stimuli (iBiology, 2014a). Or, the sensory receptors were undergoing evolution and were able to cross a threshold to be able to detect light waves, and perceive the regular and consistent scheduling of the stimuli. This is only speculation on my part, as no paper has described these clocks in this way.

The detection, perception, and interpretation of light qualities in the context of timekeeping is not quite vision, though there have been papers indicating a direct link between vision and circadian rhythms. In *Drosophila* the gene that maintains circadian

cells in neurons which are directly linked to photoreceptors (Helfrich-Forster, et al., 2001; Vinayak, et al., 2013), is directly linked to the strength of rod-cone gap junction couplings (Ribelayga, Cao, & Mangel, 2008).

(Apparently Blue-light reception and circadian clocks coevolved- according to Gehring, 2014).

Under phototaxis, light sensitive molecules can direct an organism toward or away from the light source, and phototropism is the plant cell behavior in the presence of light, usually growth oriented towards the light source (Fernald, 2004; Foster, 2009; Gehring, 2014; ScienceHook, 2016; Stevens, 2013; Yamaguchi, Desplan, & Heisenberg, 2010; Yong, 2016). Basic phototaxis is the use of the whole organism's response and detection, such as in some prokaryotes. These simple light sensing systems have high thresholds for behavior activation, and the light source cannot be accurately determined in these simple systems. Eukaryotes were able to localize the light sensing receptors into an "eye spot" (Shadowing) where direction of light could be determined in water in three dimensions (Arendt & Wittbrodt, 2001; Arendt, 2003; Arendt, Hausen, & Purschke, 2009; DonExodus2, 2008; Fernald, 2006; Gehring, 2014; Nat Geo Evolution, 2016; ScienceHook, 2016), and this orientation was directly synapsed to any cilia to produce movement (ScienceHook, 2016).

This is not vision, as detecting the surroundings to form an image would qualify, this phototaxis is one step below true vision.

The selective evolutionary forces on light-sensing receptors to produce photosensory proteins is the use of sunlight as energy, and the avoidance of UV damaging light (Gehring, 2014). The evolution and development of a sensory spot, or

single reception point, to detect light had to form. These cyanobacteria formed "eye spots" for a selective advantage to be able to hide from harmful UV light, or orient to a light if photosynthesis was the goal. In cyanobacteria circadian clocks, and phototaxis are indicative of light sensing ability (Gehring, 2014).

To correct the DNA damage by the UV radiation, photolyases- a DNA repairing enzyme mediated by light- evolved, and must have evolved early in the life history record, because these enzymes are found in nearly all species of prokaryotes and eukaryotes. Cryptochromes (which can detect blue, red, and far red wavelengths), are structurally similar to the photolyases, but they have only been found in most animals, higher plant species, and only a few prokaryote/eukaryote. For this spotty diversity to arise, then cryptochromes emerged three separate times, in three different clades (Gehring, 2014).

Rhodopsins are trans-membrane proteins that create a pocket for the chromophore (retinal) is bound. The diversity of rhodopsins are limited- and will be discussed in greater detail with opsins- to two major categories; 1) microbial, and 2) animal (Gehring, 2014).

Additional axonal circuits developing (Figure 4) and increase in photoreceptors (Arendt & Wittbrodt, 2001; Arendt, 2003; Arendt, Hausen, & Purschke, 2009), further diversify and refining visual information processes and the eye.

4.2. Multiple origins hypothesis vs. 'Master' regulatory conservation.

In von Salvini-Plawen & Mayr's (1977) paper (as described in Fernald, 2000) compared the individual components of the varieties of eyes, such as structure,

photoreceptor types, axon positioning, among others, and concluded that eyes had evolved 40 different times, and possibly more in evolutionary history (denoted as a 'multiple origins hypothesis'). This seminal paper's evidence has been called in to question by Gehring & Ikeo (1999) (reviewed by Fernald, 2000), as they isolated a 'master' regulatory gene for eye development *Pax-6* (Arendt & Wittbrodt, 2001; Arendt, 2003; Arendt, Hausen, & Purschke, 2009; Blanco, et al., 2009; Czerny, et al., 1999; Vopalanski & Kozmik, 2009). This 'master' gene is perpetuated and conserved across many populations, and the cloning of a *Drosophila Pax-6* and inserting it into another species (and vice versa- Gerhing and his collaborators use many different species (Gehring & Ikeo, 1999; Gehring, 2005)), the structural control remains, or is destroyed if a mutated *Pax-6* gene is used. Gehring even expressed surprise that a *Pax-6* gene was retained in a nematode that had lost it eyes due to life history evolution. And that nematode- *Pax-6* was viable when cloned in *Drosophila* (Gehring, 2005).

Interestingly in 2008, von Salvini-Plawen published another paper, which conceded their previous 1977 paper's polyphyletic model of eye emergence was a shortsighted hypothesis. Yet, von Salvini-Plawen (2008) also rejects Gehring's two-cell proto-eye model, and describes a modified theory which uses eye genes in combination with the previous polyphyletic hypothesis components that have not been disproven.

So if this eye regulation gene is conserved, and detected (sometimes in homologue or mutated form) across the different clades of phylogenetic evolution of eyes. So *Pax-6*, by this logic, must have evolved before divergence of humans, mice, *Drosophila*, etc.

4.3. Eye divergence & development.

From the fossil records (and current diversity of eye morphology) it was determined that there are two major classifications of eyes: camera-lens and compound. The structural composition of these classes are variable, but predictable. If there were other classifications to eye morphology there were too few in number to exist in the fossil record, could not be documented in the fossil record, and/or did not sufficiently create fitness benefits to pass down hereditarily. There are a further four to five sub-classifications to indicate complexity levels of the two classifications (Land & Nilsson, 2012). For example in camera-type eyes, the receptors are located in a concave pit, individually specialized to detect wavelengths of light (DonExodus2, 2008; ScienceHook, 2016), a focus and lens are sometimes included to add additional complexity. And in compound eyes the overall convex structure is broken down into individual eye units (facets) called ommatidia, and each facet acts as its own eye with a range of separate receptors in each facet, Figure 2B.

These two classes of eyes will be further explained below.

4.3.1. Compound eyes.

The first eyes in the fossil record were compound eyes from trilobites (Nat Geo Evolution, 2016). Some fossils are so well preserved that individual facets from each eye can be counted in rows and analyzed. This analysis shows that the trilobite secreted calcite (a mineral) to form its ridged outer shell, and its compound eyes, which would be designated as rock eyes, for their ridged form and formation through a mineral (Nat Geo Evolution, 2016). With contemporary compound eyes the individual facets are called

ommatidia and are not usually made up of ‘rock’ (though rock eyes still exist). Ommatidia diameter or quantity are the major causes of evolutionary divergence of insect species, with species specific specifications developing later (Briscoe & Chittka, 2001; Goldsmith, 2013; Gonzalez-Bellido, Wardill, & Juusola, 2011; Harzsch, Melzer & Muller, 2007; Posnien, et al., 2012), see Figure 2.

Each ommatidia is structured as a ‘mini-eye’ that contains some group of photoreceptors (the number varies on species), and usually a lens (Erclik, et al., 2009; Goldsmith, 2013; Harzsch, Melzer & Muller, 2007). The photoreceptors found in compound eyes are usually classified as rhabdomeric photoreceptors (named for the line of evolutionary divergence), which combine this divergence with unique phototransduction cascades, opsins and coupled proteins that are distinct from camera-lens eyes and the ciliary photoreceptors usually attributed to them (Erclik, et al., 2009; Gonzalez-Bellido, Wardill, & Juusola, 2011; Harzsch, Melzer & Muller, 2007).

There are two major optical types of the compound eyes; apposition eyes and superposition eyes (Land & Fernald, 1992). These types can be further sub divided into specialized forms (Beersma, Stavenga & Kuiper, 1975; Borst, 2009; Eye wiki, 2016; Goldsmith, 1990; Goldsmith, 2013; Hardie, 1985; Land & Fernald, 1992; Land & Nilsson, 2012; Lunau, 2014), though some debate occurs on a third major type, which I am classifying as a sub type here- neural superposition.

Apposition eyes are classified as the simplest of the compound eyes (and potentially the ancestral compound eye), with each ommatidium structured by a lens forming an image on a rhabdoms directly under the lens, by light only in one direction for each facet (Beersma, Stavenga & Kuiper, 1975; Borst, 2009; Erclik, et al., 2009; Eye

wiki, 2016; Goldsmith, 1990; Goldsmith, 2013; Hardie, 1985; Harzsch, Melzer & Muller, 2007; Land & Fernald, 1992; Land & Nilsson, 2012; Lunau, 2014). These individual images are collected by each ommatidia and collectively processed in the brain.

Superposition eyes are specialized into two sub categories; optical and neural. Optical (refracting) superposition eyes have a gap between the rhabdoms and the lenses, though the directional light is filtered through many lenses and focused into one set of photoreceptors in one ommatidium. The neural (open-rhabdoms) superposition eye is structured like the apposition compound eye, but while the photoreceptors are isolated in individual ommatidium, the parallel optical axes that the photoreceptors intersect on with the neighboring ommatidium to pool collective information into the same neuron (Eye wiki, 2016; Goldsmith, 1990; Goldsmith, 2013; Land, 2005; Land & Nilsson, 2012; Lunau, 2014), though this is considered a variant of apposition eyes too.

There is a third mentioned superstition eye (parabolic) that uses refractive mirrors to focus the image, though active information was lacking, and many papers did not make the distinction between this sub-category and other superposition eyes (Borst, 2009; Eye wiki, 2016; Goldsmith, 2013; Hardie, 1985; Land & Fernald, 1992; Land, 2005; Land & Nilsson, 2012; Lunau, 2014). And other specialized eyes were mentioned as ‘in-between compositions’ of different combinations of the types of compound eyes (Eye wiki, 2016).

4.3.2. Camera-type eyes

An easier to describe eye is the Camera-lens type, because humans possess two of them. It is far easier to understand a sense when it can be easily analogue to a sense the

researcher already possesses. Distinct from the convex compound eyes, the Camera-lens eyes are concave, and mostly associated with vertebrates.

Starting from the primitive eyespot, a concave cup-like dip in the photosensitive cells creates directional localization of light and shadow, and constricting the opening that light can enter and activate those photosensitive cells specializes greater tracking of movement, though this image is dim- this eye is considered a pin-hole eye. Once a lens develops over the pin-hole/opening, the light can be focused on the retina, and the more convex a lens is, the sharper the images becomes. Further developments such as iris control, muscles to move the eye, binocular overlap, and neural connectivity (C0nc0rdance, 2009; DonExodus2, 2008; Erclik, et al., 2009 Handwritten Tutorials, 2014; Handwritten Tutorials, 2011b, 2011c; Jean, Ewan, & Gruss, 1998; Lamb, 2009; Lamb, 2013; Land & Fernald, 1992; Land & Nilsson, 2012; Martin Shapiro, 2013; Nat Geo Evolution, 2016; Poejavlo, 2012; Rich Radke, 2015; Sanes & Zipursky, 2010; ScienceHook, 2016; Sinn & Wittbrodt, 2013; TED-Ed, 2015; Williams, de Wit, & Ghosh, 2010; Yong, 2016), see Figure 3.

The architectural ability of one lens which filters to an array of repeating photoreceptors in the eye is different from the compound eye of individual facets of ommatidium. In the camera-type eye there are two major ciliary-photoreceptor types; rods and cones. The number and density of these rods and cones vary with species and eye type, but generally rods are correlated with the scotopic visual system for movement, circadian, and ‘monotone’ tracking, where cones are the phototropic system which includes color vision (Adler & Canto-Soler, 2007; Bowmaker, 2008; CrashCourse, 2015; DonExodus2, 2008; Ebrey & Koutalos, 2001; Fernald, 2000; Fernald, 2006; Gehring,

2014; Goldsmith, 2013; Imamoto & Shichida, 2014; Jean, Ewan, & Gruss, 1998; Lamb, 2013; Land & Fernald, 1992; Land, 2005; Land & Nilsson, 2012; Nilsson, 2009; Pichard, Briscoe & Desplan, 1999; Rich Radke, 2015; Sanes & Zipursky, 2010; Sinn & Wittbrodt, 2013; Soloveni, et al., 2009; Volpalensky & Kozmik, 2009; Warrant, 2009; Williams, de Wit, & Ghosh, 2010). Some varying combination of the photoreceptor families dictate the varieties of vision that camera eyes have to offer.

Both of these eye types are distinct because they diverge in the evolution of opsin, the opsins activated and used, the photoreceptors accumulated, how the photoreceptors are manipulated, and which genes control eye development.

4.4. Opsins.

The newest branch of vision research has been the opsin documentation and discovery. In light sensing systems of animals, it is the opsin protein class that is the root of all systems. The opsin is activated by a light sensitive vitamin A derivative (Land & Fernald, 1992; Land & Nilsson, 2012; Terakita, 2005). In animals this is a G protein-coupled reaction - GPCR (or stimulus cell-membrane reaction) - intersecting the membrane in seven helical parts. In photoreceptors an opsin is attached to a chromophore (a ring molecule attached by a Schiff Base linkage to the opsin protein) is light sensitive, and it can alter the shape of the opsin depending on the wavelength of light that has activated it (Brown, Salgado & Struts, 2010; Deupi, 2014; Handwritten Tutorials, 2011a; Kelber, Vorobyev & Osorio, 2003; Shichida & Matsuyama, 2009; Stevens, 2013; Terakita, 2005). This action is phototransduction, which isomerizes (changes the arrangement of) the photometer by the photon, causing an enzymatic cascade (forward

moving cellular reaction) (Arshavsky, Lamb & Pugh, 2002; Ebrey & Koutalos, 2001; Fernald, 2006; Gehring, 2014; Gunkel, et al., 2015; khanacademymedicine, 2013c; Lamb, 2013; Porter, et al., 2012; Satoh, et al., 2010; Shichida & Matsuyama, 2009; Volpalensky & Kozmik, 2009; Yau & Hardie, 2009; Yildiz & Khanna, 2012; Zucker, 1996). The altering of the opsin is the transfer of light to neural signals that are processed in the brain (Cronin, et al., 2014; Ebrey & Koutalos, 2001; Fernald, 2006; Frentiu, et al., 2007; Gehring, 2014; Koyanagi & Terakita, 2014; Wernet & Desplan, 2004; Yildiz & Khanna, 2012; Yong, 2012).

While opsins are the most common protein for light sensitivity, they are distinct from photoreceptor cells. The opsins are contained within the photoreceptor cells, and each photoreceptor cell is generalized or specialized to activate the opsins at different wavelengths of light (Ebrey & Koutalos, 2001). In vertebrates the photoreceptor cells are generalized into rods and cones, and in invertebrates these cells are called rhabdoms (Cronin, et al., 2014). In cones the different types of opsins are separated and then grouped together, so only the opsins that are activated by one wavelength range are in one cone type, and another opsin class in another. In rhabdoms there are 8 to 9 classes (not subfamilies, or sub-groups) of opsins are composed into one ommatidia. That ommatidia is repeated in the compound eye of insects in each facet from one to over 10,000 facets per compound eye (Briscoe & Chittka, 2001). Photoreceptors will be discussed in section 4.6.

4.4.1 Evolution.

Morgan's Cannon (or Last Universal Common Ancestor) (Land & Nilsson, 2012; Trezise & Collin, 2005) defines that conservation is more likely than random association- the simplest answer is usually correct. A relevant example is that in visual opsin evolution the simplest explanation for visual opsins to show up in all vertebrate species is for the ancient opsin gene to have existed before vertebrates and invertebrates split into separate clades. Since the sequencing of the bovine opsin in 1982 (Shichida & Matsuyama, 2009; Terakita, 2005) thousands of opsins have been found, from insects to mammals and even fungi (Idnurm & Howlett, 2001).

While this paper will focus on the role of opsins as light sensors in visual systems, it should be noted that there are thousands of sequenced opsin genes, which are categorized into two types, and between six to eight sub-families combined in those types for opsins. Some of the sub-families have further division into subgroups, and in the subgroups of opsins only three directly participate with visual light sensing. Other subfamilies and subgroups function in a variety of non-visual ways, such as pigment control and circadian rhythm regulation, and some opsins have not been studied enough to determine their function (Bao & Friedrich, 2009; Collin, et al., 2004; Craig Blackwell, 2013h; Ebrey & Koutalos, 2001; Fernald, 2006; Fryxell & Meyerowitz, 1991; Hering, et al., 2012; Kattie, et al., 2010; Koyanagi, et al., 2008; Koyanagi & Terakita, 2014; Lamb, 2013; Land & Nilsson, 2012; Nilsson, 2009; Peirson, Halford & Foster, 2009; Shichida & Matsuyama, 2009; Soni & Foster, 1997; Terakita, 2005; Zhang, et al., 2011). Opsin subfamilies do have distinct parameters for classification, according to Terakita (2005) there are less than 25% similarity in the opsin genes between subfamilies, and greater than 40% similarity within subfamilies when seven subfamilies were determined. Soni &

Foster (1997) noted that subfamilies of vertebrate opsin had 65% similarity between each other and a 95% similarity within. Shichida & Matsuyama (2009) determined that six subfamilies of opsins show less than 20% identity between each other. While there is some discrepancy as to how many subfamilies opsins should be divided into, there is a similarity in the divergence that subfamilies are classified by (Henze, et al., 2012), and similar subfamily labels are consistent.

Type 1 opsins are microbial, and type 2 opsins are (mostly) vision oriented (Craig Blackwell, 2013h; Fernald, 2006; Zhang, et al., 2011). Both types are considered to be conserved helical homologues, despite functional diversity (Gehring, 2014). Type 1 opsins (microbial opsins) are the older of the two, found in archaea and eukarya, and probably existed before the archaea/ eubacteria /eukaryote divergence, and there is evidence suggesting the existence prior to even photosynthesis (Fernald, 2000; Fernald, 2006; Gehring, 2005; Gehring, 2014; Zhang, et al., 2011). Type 2 opsins (Animal opsins) are mostly attributed to the three phyla of visual light-detection/sensing/transducing image forming eyes (Frentiu, et al., 2007b).

With the common chain of opsin conservation, dating its evolution can be inferred that the ancient form of opsin existed before the divergence of fungi, and as Lamb (2013) argues, even earlier: before the amoeba-like placozoans diverged (Fernald, 2006; Land & Nilsson, 2012). The divergence of opsin families is depicted in Lamb (2013) as a speciation towards light receptive opsin genes, however it is relevant to opsin history to focus on vision evolution as the genetic changes are better known and documented in vision than other opsin based expressions (Koyanagi, et al., 2008; Lamb, 2013). As opsin expression can vary in sensitivities by single amino acid variations, which those

expressions should be taken within the context of the visual system it is being expressed in.

Before vision diverged, it is theorized that opsins that had preferences for different membranes and once a genetic shift occurred subfamilies would begin to form. These subfamilies would be distinguished by the location of the opsin in a cell; some opsin genes remained on the surface of a cell, and others were membrane bound on organelles within the cell. Then a second duplication event occurred specializing the opsin further to which surface membranes the opsin would be embedded in (Goldsmith, 2013; Lamb, 2013; Neitz & Neitz, 2011). It is with further "Division of Labor" that the Rhabdomeric (r-opsins) and Ciliary (c-opsins) could diversify again and again (Vanfketeren, 1982).

Ciliary opsins (c-opsins) are the precursor to most deuterostome, light-sensitive photopigments, and microvilli are the protostome (Goldsmith 2013). Generally this can be taken as the divergence of compound and camera eye types. And taking the ciliary diversification further will help explain. Leading up to the diversification of vertebrate C-opsins, the ciliary photoreceptors of chordate are classified into gradated groups of performance and specialization (Lamb, 2013). This indicates what systems of photoreceptors are seen at the different junctions of chordate groups: though the Hagfish is more of a "de-evolution" it represents an in-between evolutionary marker. Figure 4 indicates the morphology of the different cordate photoreceptors. At each stage of evolutionary history some system was being altered, form more efficient transmission, to the division of labor (Lamb, 2013; Cook & Desplan, 2001).

Recent research has indicated that while it is generally assumed that ciliary-opsins diverged from rhabdomeric-opsins, there have been cases of ciliary-opsins in rhabdomeric eyes, and rhabdomeric structures in lens eyes (Peirson, Halford & Foster, 2009; Stevens, 2013), though this is not common. Stevens (2013) has indicated that categorizing photoreceptors by cascades or opsin families (Lamb, 2013) may be a more efficient way to categorize these systems, but has not been used in the past often. In vertebrates ciliary-types are more common, and in invertebrates the rhabdomeric structures are more pronounced (Stevens, 2013).

Rods evolved from cones (Collin, et al., 2004; Ebrey & Koutalos, 2001; Lamb, 2009; Lamb, 2013; Shinhida & Matsuyama, 2009; Warrant, 2009; Yau & Hardie, 2009). Rod and cones have the same sensitivity to light, the difference is the prolonged sensitivity state of the rods vs. cones. The rods are effected longer then cones by being activated by the light.

Visual pigments are evolutionarily related (Cronin, et al., 2014). In Shinhida and Matsuyama (2009) evolution experiments over the opsin where vertebrate and rod opsins are different evolutionary histories. In vertebrates a counterion was evolved to stabilize the transmembrane of the opsin-retinal attachment, which is unstable normally. This counterion has not been proven to exist directly in experiments yet.

It is assumed a photoreceptor can only express one opsin and one visual pigment (this has been proven false, but is a simplified explanation to delve into to build on).

4.4.2. Structure.

This protein is a 7-transmembrane- amino acid chain, that is depicted Figure 5, and directly interacts with wavelengths of light to change structure depending on the specific wavelength it is interacting with.

4.5. The genes of eye morphogenesis.

In the previous section 4.2. Gehring & Ikeo's (1999) paper was used to discuss the isolated "master" gene that controls eye development: *Pax-6* (Arendt & Wittbrodt, 2001; Arendt, 2003; Arendt, Hausen, & Purschke, 2009; Blanco, et al., 2009; Czerny, et al., 1999; Vopalanski & Kozmik, 2009), this gene is also written as *pax6 (*which I will be using), *Pax6*, *pax 6*, and *Pax 6* in other research papers. This gene is conserved across many species and phyla (Arendt & Wittbrodt, 2001; Arendt, 2003; Bao & Friedrich, 2009; Bazin-Lopez, et al., 2015; Blanco, et al., 2009; Fernald, 2006; Gehring & Ikeo, 1999; Hoshiyama, Iwabe & Miyata, 2007; Kozmik, et al., 2003; Rister, Desplan, & Vasiliauskas, 2013; Treisman & Herberlein, 1998; Weasner, et al., 2009; Yang, et al., 2009a; Yang, et al., 2009b), though there is one paper that debates the last common primordial *Pax* gene is a *PaxB*-like gene, due to the *PaxB* gene being found in jellyfish, and the last common ancestor of jellyfish and other eye phyla was when cnidarian and triploblasts diverged, the paper argues that *Pax6*-like genes evolved after the divergence in triploblasts, and triploblasts eyes arose independently in cnidarian species (Kozmik, et al., 2003). Despite this paper, the *pax6* homeobox (or *Pax* homeobox) genes are grouped to represent the conservation of the *pax6* gene in eye development. *Drosophila* have *pax6* orthologues (called *eyeless* (*ey*) and *eyegone* (*eyg*)) that are found in the entire eye disk formation, and other *pax6* orthologues in eye precursor cells *(twin of eyeless* (*Toy*), *twin*

of eyegone (*toe*), *eyegone (eyg*)) and eye formation, with direct connections to photoreceptor cells in some cases. This is probably an evolved function as *pax6* family genes have been found in non-eye forming species with no photoreceptor connection or regulation. Additionally the *toy* gene is found in the *Drosophila* genome upstream of the *ey* gene, and *toy* is necessary to initiate the production of *ey* transcription factors, which have been shown in ancestral like species to exist in a state of redundant control (Arendt, 2003; Czerny, et al., 1999; Yang, et al., 2009b).

Though since the Gehring & Ikeo (1999) paper other genes have been found to be necessary in eye development, though some genes do vary between phyla and species (Adler & Canto-Soler, 2007; Amore & Casares, 2010; Fernald, 2006; Weasner, et al., 2009). The *six/sine* oculus gene family is independent of the *pax6* gene family but is common in eye development of insects, vertebrates and planetarians (Arendt & Wittbrodt, 2001; Arendt, 2003; Hoshiyama, Iwabe & Miyata, 2007), and many *six* genes are found in late stage eye development and are expressed differently across species. *Six1/2* orthologues for instance are late expressed transcription factors for eye development, *six2* in vertebrates is specifically expressed in photosensitive cells, and *six3* appears to assist in anterior brain development and work independent of *pax6* (Arendt, 2003), and *sine oculis (so*) is the *Drosophila* orthologue to this gene family, which is activated by *toy* (Arendt, 2003; Blanco, et al., 2009; Moses, 2002), and *Optix* genes which are included in eye field specification genes.

Orthodenticle (otx) genes are expressed differently from the *six/sine* and *pax6* gene families. The *otx* genes are part of a larger *OAR (Otx/odt, Arx/crx,* & *Rax/Rx*) family and appear conserved for photoreceptor and eye development in many, if not all, retinal

cells (Adler & Canto-Soler, 2007; Arendt, 2003; Bazin- Lopez, et al., 2015; Blanco, et al., 2009; Fernald, 2006; Janssen, Budd & Damen, 2011; Moses, 2002; Rister, Desplan, & Vasiliauskas, 2013). *Otx2* in early eye development regulates forebrain development (where eyes usually develop), *Rx3* influences cell migration during optic cell evagination (Adler & Canto-Soler, 2007), and help regulate *ephs* & *ephrine* gene families, and keep eye field and the anterior neural plate segregated (Bazin-Lopez, et al., 2015). *Crx* and *Otx2* in later eye formation are directly linked to rod and cone photoreceptor determinations in vertebrates (Arendt, 2003). *Odt* are specific to *Drosophila* compound eye formation, which regulates *eya* expression through *Wingless (Wg*) signaling inhibition and *Hedgehog (hh*) signaling expression (Blanco, et al., 2009). *Odt* in *Drosophila* also regulates the opsin genes *rh3* and *rh5* by activation (Rister, Desplan, & Vasiliauskas, 2013).

Ski family genes are transcriptional factors that regulate cell transformations in vertebrates (Moses, 2002). The *dac* gene is required for normal eye formation, but is not as essential as *eya* or *so* in *Drosophila*, it does show regulation of ommatidium segmentation and specification, and works in tandem with *ey* and *toy* (Blanco, et al., 2009; Moses, 2002; Yang, et al., 2009a), and also can be found in helping to form the kidney, muscle tissue, and the inner ear (Fernald, 2006).

The *eya* gene family, specifically the *eya* gene is necessary for normal eye development, and is usually discussed in tandem with the *so* gene (even if they are in different families). *Eya* or *so* deleted mutants are lethal as most of a face is missing (usually) from development, additionally any regulatory deletions of genes that go with either gene creates an eyeless phenotype, though still living. *Ey* genes directly regulate

eya genes, and if *ey* is absent then *eya* will produce an eye larger than normal, but overexpression of *ey* or miss-expression of *eya* will cause smaller than normal eyes (Moses, 2002; Yang, et al., 2009a). *So* genes are activated by *toy* genes and then dependent on *eya* genes to properly maintain their feedback loop for production of transcription factors (Blanco, et al., 2009).

Teashirt (TSH) genes in *Drosophila* are for embryo development for trunk segmentations, and produces a transcription factor with zinc-finger motifs that induces activation of *ey*, *so*, and *dac* genes, and in a feedback loop *ey* induces *tsh* to express (Gehring & Ikeo, 1999). Mutant *tsh* genes in the antennal disk formation cause *ey*, *dac* and *so* expression to form eyes on the antennae of *Drosophila*, but knockout mutants of *tsh* form eyes fine with antennae, so it has been proposed that *tsh* has no direct link to eye formation, however it is also possible that *tsh* is a redundant gene (Moses, 2002). Though not expressly detailed, but from Moses (2002) to Blanco, et al., (2009) *tsh* is no longer discussed in any paper I have read. Moses (2002) speculated that *tsh* was redundant to the transcriptional factor *cubitus interriuptus (Ci*), which are also zinc-finger motifs. *Ci* transcriptional factors are regulated by the *hedgehog* signaling pathway, and the full form of the *Ci (Ci155*) activates the *eya* gene, which causes cell clusters to form with either *so* or *eya* expression (ocelli primordium). Signaling molecules *DPP* and *Wingless (Wg*-which works in antiasthma to *DPP*) assist in segregating the eye field with other genes (such as *ey*) for cell fate determinations. Since the *Ci* has accumulated in its activator form (*Ci155)* in the primordium, *hh* then cleaves the transcriptional factor into *Ci75*, which then inhibits *DPP* and *eya* so the *Ci75* can induce photoreceptor cell differentiation (Amore & Casares, 2010; Blanco, et al., 2009). While Blanco, et al. (2009)

never mentions *tsh*, it is possible that *tsh* has been renamed as one of the two operating forms of *Ci* (I would assume *Ci155*), but that is only speculation.

TRX (Iroquois) are a gene complex in *Drosophila* compound eyes that control the transcription factors that regulate the dorsal/ventral fields of the ommatidium in eye differentiation (Dominguez & de Celis, 1998).

These genes and gene families are only reflective of acting in the formation of eye morphology, and many genes also are part of the neural network formation and differentiation which will be looked at in detail later.

4.6. Photoreceptors.

While opsins are the most common protein for light sensitivity, they are distinct from photoreceptor cells. The opsins are contained within the photoreceptor cells, and each photoreceptor cell is generalized or specialized to activate the opsins at different wavelengths of light (Ebrey & Koutalos, 2001). In vertebrates the photoreceptor cells are generalized into rods and cones, and in invertebrates these cells are called rhabdoms (Cronin, et al., 2014). In cones the different types of opsins are separated by activated wavelength and grouped together by the same activated wavelength, so only the opsins that are activated by one wavelength range are in one cone type, and another opsin class in another. In rhabdoms there are 8 to 9 classes of opsins are composed into one ommatidia. That ommatidia is repeated in the compound eye of insects in each facet (Briscoe & Chittka, 2001).

As indicated above, increasingly complex tasks in visual behavior would drive the evolutionary complexity (Land & Nilsson, 2012). In the case of detecting light intensity

and movement, only one type of photoreceptor is necessary, while color vision requires two or more types of photoreceptors. In terms of prey (or predator) detection (Arendt & Wittbrodt, 2001; Arendt, 2003; Baden, et al., 2013b; Endler, 1991; Houde, 1997), the movement of an object can take precedence over what color the object is (Melin, et al., 2006), whereas determining fruit ripeness, or other food colors indicative of more nurturance, it is necessary for survival purposes and would require two or more photoreceptor types (Nat Geo Evolution, 2016). Each is a complex component of vision, but requires different levels of complexity and bias to function. Further complication arises when both signals are received along the same pathway. The innate bias of reception of color over movement, or vice versa, is dependent on the evolutionary history of the population.

4.6.1. Evolution.

For most of photoreceptor evolutionary history, opsin evolutionary history is the star. As opsins are a key component of photoreceptors, and their activation by light is the highlighting goal of most photoreceptors, the emergence of an opsin gene would predate the structure of a photoreceptor. As explained above in the common chain opsin evolutionary development, and the conflicting theories in when the two classes (rhabdomeric vs ciliary) diverged can carry the evolution of photoreceptors to a common point of the deuterostome/protostome divergence (Bao & Friedrich, 2009; Collin, et al., 2004; Cook & Desplan, 2001; Craig Blackwell, 2013h; Ebrey & Koutalos, 2001; Fernald, 2006; Fryxell & Meyerowitz, 1991; Gehring, 2014; Hering, et al., 2012; Kattie, et al., 2010; Koyanagi, et al., 2008; Koyanagi & Terakita, 2014; Lamb, 2009; Lamb, 2013;

Land & Nilsson, 2012; Nilsson, 2009; Peirson, Halford & Foster, 2009; Shichida & Matsuyama, 2009; Soni & Foster, 1997; Terakita, 2005; Zhang, et al., 2011). In Gehring (2005) two major hypothesis for animal photoreceptor origins are put forth; 1) the cell differentiation model, and the 2) symbiosis model.

In the cell differentiation model assumes an ancestral colony of flagellate-like cells is the precursor to all animals. This colony has many cells, all of which possess an 'eyespot' (a photoreceptor organelle), this eyespot is used to convert photons to mechanical movement, which then uses the connection to a flagella for phototaxis. This colony then undergoes a population wide differentiation (through evolutionary time) so unicellular photoreceptors are present in a ciliated membrane, with each photoreceptor possessing a visual pigment, microvilli, melanin pigment granules, and cilium. After this the evolution of the unicellular photoreceptors would differentiate into the two cell types (pigment cell and photoreceptor cell) of the proto-eye (Gehring, 2005; Lamb, 2009).

The symbiosis model (also known as the Russian doll model) goes further back to cyanobacteria, and the presumed emergence of light-sensitivity. These light sensitive cyanobacteria were (at a random point) eaten but not digested by a red algae (eukaryote) that then used the cyanobacteria as a primary chloroplast, surrounded by two membranes. Later on a cyanobacteria engulfed by a red algae was taken up by dinoflagellates as secondary chloroplasts, which have four membranes surrounding the system. Some species of dinoflagellates would take their four membrane secondary chloroplasts and evolve/transform the system to a pre-photoreceptor organelle, and the others continued to use photosynthesis. The dinoflagellates that had the pre-photoreceptor organelles are assumed to have transferred the genes to cnidarians as dinoflagellates are symbionts

among cnidarians, which is the most unlikely part of this model. This model uses this transfer of genomic information as the explanation for the random emergence of photoreception at different points in time among different groups of cnidarians (Gehring, 2005).

For simplification, due to genetic analysis and debate, it can be inferred that the ciliary and rhabdomeric/microvilli photoreceptor cell types probably emerged from a precursor photoreceptor cell (Fain, Hardie, & Laughlin, 2010), and either/both of those cell types are described in almost all phyla. Ciliary photoreceptors use either the c-opsins or the G (subscript 0)-opsin, and the rhabdomeric photoreceptors exclusively use r-opsin. It can be implied that these strict combinations of [photoreceptor + opsin] division occurred before the bilaterian/cnidarian split. In most cases once photoreceptor cell type will become the sole visual-photoreceptor, while the other will develop into a non-visual role, or become a complementary or assessor system to the visual-photoreceptor type (Fain, Hardie, & Laughlin, 2010; Lamb, 2009; Vopalensky & Kozmik, 2009).

In the case of the rhabdomeric-photoreceptor (r-PR) cells, these have become the primary visual photoreceptors in most invertebrate species. This may be due to the r-PRs high sensitivity, large responses to singular photons, and the outperformance in cascade speed in dim and daylight conditions compared to invertebrate ciliary-photoreceptors (c-PRs). In invertebrates the c-PRs are limited in function, range, intensities, and cannot transition from dim to daylight conditions (Ebrey & Koutalos, 2001; Fain, Hardie, & Laughlin, 2010; Lamb, 2009; Lamb, 2013).

However the ciliary-photoreceptors dominated the chordates probably due to the development of the ‘rod-like’ photoreceptor. The low-sensitive ‘cone-like’ c-PRs in

invertebrates combined with the new highly-sensitive ‘rod’ c-PRs to create a full range of sensitivities; the duplex retinae [rods + cones]. Further the duplex c-PRs are cheaper energetically over r-PR, because the r-PRs are constantly active and c-PRs can ‘power down’ the rods when dim-light is not present, so the low sensitive (low energy) cones are active. Ciliary-PRs are cheaper still due to more efficient photon tracking/counting in a given space compared to r-PRs, requiring less energy for guessing, and it is possible c-PRs were bettered suited for shadow detection (Ebrey & Koutalos, 2001; Fain, Hardie, & Laughlin, 2010; Lamb, 2013; Nilsson & Arendt, 2008), see Figure 4.

Rod emergence occurred recently after the four precursor cone opsins had formed (Lamb, 2009). This is due to need for high gain in single photon activation, and while this emergence occurred recently in vertebrate duplex retina, a duplex in a jawless model species for pre- jaw/jawless ancestral divergence, though the lamprey visual system is mostly cones, the duplex cone/rod distinctions comes from the single photon activation. So it is possible that the duplex ability of the retina emerged and developed before the jaw/jawless divergence, though not before rods appeared in the evolutionary record (Warrant, 2015). Even more encouraging is that, in fitness standards, the rods cost less energy to maintain than cones, and so the selective pressure should have funneled to rod formation no matter the species (Warrant, 2009).

At some point during the improvement of the C-opsin, an even further ancestral Cone photoreceptor emerged. This photoreceptor was more efficient and could activate at specific wavelengths of light. Before a higher set of changes occurred, and before vertebrate diversification, this cone doubled itself into short-wavelength –sensitive (SWS) and long-wavelength-sensitive (LWS) photoreceptors. This would have allowed

for a greater range of visual perception, and an increased sensitivity to the environment (Ebrey & Koutalos, 2001; Goldsmith, 1990; Lamb, 2013; Shichida & Matsuyama, 2009).

During the Cambrian the two cone photopigments underwent two separate cases of full genome duplication. However, when the SWS and LWS duplicated a forking phyletic tree should emerge but has not (this tree is most likely monophyletic). Lamb (2013) discusses the differing selective pressures that could have caused this odd five cone system. For example; the SWS cone peak sensitivity is around 380 nm (violet/UV), then a twice doubling (and the division of labor) of the cone genome would grant a UV-SWS, the original 380 nm-SWS, and a 440 nm-SWS. In this hypothetical system there would be greater selective pressure to see more of the visual color spectrum, as (it is assumed) one UV receptor will be able to obtain the same amount of information as two UV receptors, then the second UV receptor would not be selected for (Lamb, 2013). Now that five cones are present in vertebrates (SWS1, SWS2, Rh1, Rh2, and LWS)* then color vision can be demonstrated in some narrow scope (Ebrey & Koutalos, 2001; Lamb, 2009; Nilsson & Arendt, 2008). *exception in crawfish due to the 12 photoreceptors?

In the fly there are eight photoreceptor cells that are assigned two visual pathways (Lunau, 2014; Strausfeld & Lee, 1991) which are processed in parallel. The R7 & R8 are uniquely processed, as the R1-R6 are usually combined in the activation. The R7/8 tandems can be either pale or yellow, and depends on their sensitivity which tandem the photopigments are classified on (Bishop, 1974; Hardie, 1985; Horridge & Mimura, 1975; Kirschfeld, et al., 1983; Stark, Frayer & Johnson, 1979; Tsukahara & Horridge, 1977; Tsukahara, Horridge & Stavenga, 1977; Yamaguchi, Desplan, & Heisenberg, 2010). The

pale or yellow determination has to do with which opsins is expressed in the R7/R8 photoreceptor.

Recently there have been studies which have mapped the use of non-opsin and non-image-forming photoreceptor cells, which are used in *C. elegance* and *D. melanogaster* (larva) to avoid light. Specifically the 'non canonical" systems still use a G-protein coupled pathway, but in the place of the opsin-gene, anther light sensitive protein is used (*Lite-1* or *Gr28b*) which are still activated by light, both lack any phosphor-enzymes to induce the depolarization of normal photoreceptor cells. Additionally the *Gr28b* protein cascade is missing an inducing enzyme to start the phototransduction cascade (Diaz & Sprecher, 2011). But still a photoreceptor without opsins, and without image forming mechanisms is remarkable. Though non visual opsins and melanopsin (discussed before) have been coopted for functions not involving light detection directly, such as circadian rhythms (Koyangi, et al., 2005; Lucas, 2013; Peirson, Halford & Foster, 2009), which may have been the precursor to all visual systems.

4.6.2. Structure & diversity.

Tuning of photoreceptor sensitivity requires a change in the opsin gene to change the sensitivity of the photoreceptor (Bowmaker, 2008; Collin, et al., 2009; Osorio & Vorobyev, 2005; Stevens, 2013). Further tuning can occur due to colored filters or oil drops for photoreceptors (Bowmaker, 1980; Goldsmith, 1990; Hart, et al., 2000).

In the case of oil droplets, these are found in the cones of primitive fish, which infer an ancestral/ancient cone composition which includes an oil droplet (Bowmaker,

2008). These oil droplets, which are usually colored, filter the light-stimuli to a narrowed wavelength before the photoreceptor can be activated by the stimuli (Goldsmith, 2013).

In Goldsmith (2013) the discussion of an evolutionary end results as mountain peaks on a landscape (this landscape is adaptive probabilities given genetic possibilities) (poejavlo, 2012). This mountainous peak system described as the evolutionary history of any eye system with the end peak resulting as a working eye for the environment it exists in. In this case an organism leaping from one peak to another is unlikely. This is his explanation for things like oil drops, etc. As these peaks are a result of historical evolutionary events imbedded with extinction probabilities and environmental shaping unlikely to translate correctly between species.

Photoreceptor cells have huge membranes folded for layers of perpendicular sections. In vertebrates it is ciliary lenin folded photoreceptors, in arthropods it's toothbrush structure of rhabdomeric photoreceptors. Some have filters (Cronin, et al., 2014; Soloveni, et al., 2009), see Figure 2 and Figure 3.

Photoreceptor subtype diversification and subtype specification can determine which opsin receptors are present in the corresponding photoreceptor, and this can be controlled by different transcriptional genes and activations (Arikawa & Stavenga, 1997; Ashley & Katz, 1994; Awata, Wakakuwa, & Arikawa, 2009; Beersma, Stavenga & Kuiper, 1975; Chiao, et al., 2000; Choe, et al., 2006; Chou, et al., 1996; Chou, et al., 1999; Clandinin, et al., 2001; Cook & Desplan, 2001; Cook, et al., 2003; Douglas & Jeffery, 2014; Dupuis, et al., 2012; Friedrich, 2008; Friedrich, Wood & Wu, 2011; Goldsmith, 2013; Heisenberg & Buchner, 1977; Katti, et al., 2010; Kelber, 2005; Kitamoto, et al., 1998; Kitamoto, Ozaki, & Arikawa, 2000; Kumar & Ready, 1995;

Montell, et al., 1987; Papatsenko, Sheng, & Desplan, 1997; Polaczyk, Gasperini, & Gibson, 1998; Soloveni, et al., 2009). Additionally the rate of transduction of the visual information processed can cause an increase in fitness depending on the light qualities or environmental optimums (Chittka & Menzel, 1992; Ebrey & Koutalos, 2001; Eckstien, et al., 2013; Frederiksen, Wcislo & Warrant, 2008; Goldsmith, 2013; Gomez & Thery, 2004; Gomez & Thery, 2007; Hofmann, et al., 2009; Juusola & Hardie, 2000; Juusola & Hardie, 2001; Katti, et al., 2010; Osorio & Vorobyev, 2005; Stavenga, 1992; Stavenga & Arikawa, 2011; van Hatteren, 1992).

4.7. The other genes of vision.

Though some genes and transcription factors were functionally tuned to eye morphological development and structure, as mentioned above, some genes also contributed to other tissue development, other sensory systems, and contributing to the overall health of the developing embryo (as anything is better than lethal). *Otx* genes in the vertebrates assist in the retinal ganglion development, *six3* in vertebrates contributes to brain (specifically anterior) development (Ardent, 2003). Early optic vessel neuro-epithelial cells co-express *Rx, Hes1, otx2, pax6, six9, six3* & *Lhx2* according to Adler & Canto-Soler (2007), where *otx2* and *Hes1* are non-eye field transcription factors that may contribute to the forebrain development in vertebrates. *Toy* or *eyg* mutants create a lethal (headless) embryo, *so* contributes to total head structure development in some form (Blanco, et al., 2009).

The hedgehog signaling pathway *(hh*) was used to regulate and cluster the ommatidium subtypes, and this was due to the induction of the *hh* signal along the

photoreceptor neurons, allowing for the activation of the clusters, which is the final cell differentiation to then start the neuronal targeting (Huang & Kunes, 1996).

N-cadherin genes are necessary for neuronal development between photoreceptor R-cells to properly target the appropriate brain layer for proper vision-stimuli processing and unpacking, to not reach the proper area of the brain could prevent information from being relayed properly, or not working at all. In invertebrates the *Liprin-(alpha*) is cell-autonomous in all of the R1-R6 subtypes, which allows the photoreceptor axons to reach their proper targets, with assistance from the *tyrosine phosphatase LAR receptor* (Choe, et al., 2006; Clandinin & Zipursky, 2002; Hofmeyer, et al., 2006). And the *ninaB* and *ninaD* genes are only expressed in the *Drosophila* brains (Yang & O'Tousa, 2007).

Runt and *breakless* genes are not expressed in the same R-cell axons, but work in similar regulation signaling systems for cone growth and targeting/recognition of laminal glia determinants (Clandinin & Zipursky, 2002). *PTP69D* genes are also expressed in R-cell axons and growth cones, but act during embryonic development, guiding most of the neurons to the developing central nervous system (Clandinin & Zipursky, 2002). *Dock* and *pak* genes appear to form an intermediate targeting pathway for axonal targeting of the medulla or lamia layers of the brain, and these genes along with the *Trio* (which has not been studied as thoroughly) all assist in conserving the cone R-cell growth and signal transduction pathways evolutionarily (Clandinin & Zipursky, 2002).

The genes found in rhabdomeric photoreceptors could be vertebrate ganglion cells with R-opsin expression and the *pax6, Math5, Brn3* & *BarH* transcription factors being present in both versions (Fernald, 2006).

Drosophila has an additional gene from the *WAVE/Scar* complex and *actin* family; *CYF1P/Sra-1*. This member of the remodeling regulation family controls the terminal web organization of the rhabdomere, adherens junctions, rhabdomere extension, basement membrane integrity, and retina depth. *CYF1P-SCAR-ARP2/3* is a pathway that controls and moderates the remodeling of specific tissues (such as during morphogenesis) (Galy, et al., 2011). Also in *Drosophila* a *nonA* gene, is necessary for the electrophysiological signaling to remain consistent and strong, lacking *nonA* could cause the electrical impulse to dye before reaching the target layer of the brain for processing, and the *INAD* protein helps regulate the signaling pathways in *Drosophila* (Jones & Rubin, 1990; Liu, et al., 2011).

There are potentially many other genes that may contribute to proper eye development in many different species that are not discussed here. This could be due to not finding the correct papers, the selective discussions revolve around the pax6 or opsin genes, or the gene has not been isolated and described yet. And a future review should discuss these genes in detail.

4.8. The neural network of vision.

Since the simple ‘proto-eye’ used a simplified system of a single photosensitive cell (with a shading cell) to relay light information to a motion system (usually a flagella) some assumptions can be made. This transmission system that connects the photosensitive cell to the motor cell(s) could be considered a neural network, or a primitive neural system preforming axon-like processes (Arendt, Hausen, & Purschke, 2009). This system would develop in complexity.

Any minimal eye structure is dependent on the neural components for visual analysis. So in reality there are two minimal components to the eye, plus the neural structure to form a complete visual system. Though the evolution of new neural abilities and circuits is not required to obtain information from novel photoreceptors if they arise (Skorupski & Chittka, 2011), and this will be demonstrated later.

Neurons will be described in their functional, structural, and co-operative ability in the circuitry of visual systems. Neuronal cells that operate/preform the same tasks will be grouped together into cell types, and names for these cell types will be classified to the best of my ability. However, naming neuron cell types can be complicated, as not every cell type may have been found yet, and the same cell types found in different species could have been given different names over time, and no consensus naming had yet been proposed (Masland & Chittka, 2004). As mathematical models of neural circuity and its complexity have not been described in any papers I have seen, nor has the mathematics to describe how a complex system could have come about, there is a hole in theoretical modeling. Any mathematical expressions to display neural circuitry could be used in a predictive manor for behavioral systems, color vision processing, and cognitive abilities (Chittka, et al., 2012).

Here the Human (*Homo sapiens*) and *Drosophila melanogaster* neuronal systems will be described in as much detail as is possible.

4.8.1. Model: Vertebrates.

In vertebrate neuronal circuitry, intricacy and precision dominate retinal wiring discussions, and can be represented on finer and finer scales of ‘complexity’. Almost all

neurons are clumped into three distinct layers, and interconnected by two synaptic layers (also called a 'brain'). Each of these three layers can be further arrayed into sublayers, and neuronal cell types that have been specified to preform unique functions will often be restricted to one sublayer (Baden, et al., 2013a; Gollisch & Meister, 2010; Masland, 2012). In vertebrates there have been at least 50 neuronal cell types that have been described in the vertebrate neural network (Some papers have implied there are more than 60 cell types) (Gollisch & Meister, 2010; Masland, 2012: Seung & Sumbul, 2014). Though each of these cell types cannot be analyzed in depth, specific categories of the cell types will be.

When the vertebrate eye develops, it can be classified in three stages; the first phase forms the primary structures of the eye, the second phase is the maturation of these eye structures, and the third phase is the neuronal connections that form between the retina and the "optic tectum"/"Super colliculus" (Jean, Ewan, & Gruss, 1998; Sanes & Zipursky, 2010). Signaling cascades, extracellular signaling systems, and intracellular transcription factors and their receptors direct and regulate axonal outgrowth, and cellular proliferation and differentiation (Jean, Ewan, & Gruss, 1998; Sinn & Wittbrodt, 2013; Williams, de Wit, & Ghosh, 2010).

The key neuronal structures that develop in the first phase of eye morphogenesis are the optic stalk, the optic nerve tract, and the optic cup. By the second phase the inner layer of the optic cup matures into the neuronal and glial cell types. The neuronal cell types differentiate into three classes: 1) cones & rods (light sensitive photoreceptor neurons), 2) Bipolar/horizontal/amacrine neuron cells (interneurons), or 3) retinal ganglion cells (RGCs), with each class developing at specific times during

morphogenesis, RGCs first, and photoreceptors last (Jean, Ewan, & Gruss, 1998; Reese, 2011; Sinn & Wittbrodt, 2013; Williams, de Wit, & Ghosh, 2010). In summary and in general there are six cell types in vertebrate retina that develop: 1) the photoreceptors or light sensitive receptors, 2) the RGCs also called projection neurons; 3-5) the three interneuron types, and 6) glial (Muller glia) cells (Sanes & Zipursky, 2010), see Figure 3.

These six cell types are distributed non-randomly within the three 'nuclear' layers described above. These layers contain only the neuronal cell bodies, no synapse, the plexiform layers spate the layers and contain only synapses, and no cell bodies form the cell types. The first outer layer contains photoreceptors, the inner layer contains the interneurons and glia cells, followed by the ganglion layer (RGCs and some amacrine cells). The six major cell types are able to be classified by cell subtype by grouping the cells by the analysis of their molecular expressions/compositions, their physiological construction/composition, their gene expressions, and/or their cellular structure (Sanes & Zipursky, 2010). Photoreceptors primarily from only two subtypes in vertebrates- rods and cones, though cones can be further sub-grouped by the spectral sensitives /opsin/ visual pigment they express. Approximately there are 12 bipolar cell types in mammals (Masland, 2012; Priebe & Ferster, 2012; Reese 2011; Sanes & Zipursky, 2010; Seung & Sumbul, 2014), 20 types of RGCs, and 30 types of amacrine cells.

In the outer vertebrate retinal synaptic region (the outer plexiform layer) the bipolar cells, horizontal cells, and photoreceptors are linked via electrical and chemical synapses; usually forming a multiple-connect synapse from the large photoreceptor nerve terminals and the photo-synaptic processes in the horizontal and bipolar cells (Sanes & Zipursky, 2010). The vertebrate inner retinal layer (inner plexiform layer) contain the

synapses of the retinal ganglion, bipolar, and amacrine cells which is indicative of laminar specificity (Sanes & Zipursky, 2010).

The textbook standard visual system partitions visual coding in three stages: 1) light sensed by retina, retina translates light to neuro-electro signals, and information is standardized with normalized range, 2) the retina divides the primary visual signal (think of it as a pixilated photo) into parallel info streams- each stream translates only one aspect of the original 'photo'- only one pathway transmits the red saturation, another contains only contrast information, etc. 3) the information is compiled by the cortex where it is combined to "determine boarders of objects and visual perceptions" (Masland & Martin, 2007; Masland, 2012). Specifically with neuronal cell types, there are three stages for the visual processing of the total combined cell types (Masland, 2012; Reese, 2011). The first stage is information processing by the retina, which is specifically the bipolar and horizontal cell types sampling the rod and cone photoreceptors, or the photoreceptors when activated by light convert the light energy into electrical signals, and those signals are transmitted to bipolar cells (Asari & Meister, 2014; Masland, 2012). Rods are outliers in the discussion of development as they evolved much later than cones, and their circuitry is not as complex as cones: a bipolar cell that receives information form rods only, has a modulated output due to an amacrine cell, a second amacrine cell feeds the modulated output of the 'rod-system' into the same circuitry that processes cone information. Inhibitory feedback in rods and cones is controlled by horizontal cells, to gain control of the signals (Asari & Meister, 2014; Masland, 2012; Reese, 2011). Bipolar cells transmit the electrical signal obtained from the photoreceptors (and modified by bipolar/amacrine interactions) to ganglion cells in the inner retina (Asari & Meister,

2014; Masland, 2012). Unless the bipolar cell has been specialized (i.e. rod-only or blue-cone only) it is a generalized rule that bipolar cells are cross connected to cones of different specialized sensitivities, and each cell type is distinct by which information is obtained from their cross connected photoreceptors, and sent on (Masland, 2012; Priebe & Ferster, 2012; Reese, 2011; Sinn & Wittbrodt, 2013; Williams, de Wit, & Ghosh, 2010).

Synaptic neural connections are spontaneously patterned by retinal waves. These waves are coupled to visual circuit refinement; the waves disrupt/decouple neuronal activity, and new neuronal activity can create new synaptic formations/circuitry rewiring after the retinal waves have gone, indicating a synaptic plasticity of neuronal rewiring (which is controlled by retinal acetylcholine receptors) (Burbridge, et al., 2014; Janssen, Budd & Damen, 2011).

There are a small number of isolated retinal ganglia that have been found in mammalian's inner retina that are uniquely photosensitive. When they have been isolated from other photosensitive cells (can the corresponding retinal neurons) these ganglion still respond to light autonomously; named intrinsically photosensitive retinal ganglion (ipRGCs) (Emanuel & Do, 2015; Lucus, 2013).

4.8.2. Model: **Drosophila melanogaster.**

In general the nervous system of insects is classified into three ganglion segments; 1) head (usually 'one head' also called simply 'the brain', which is further portioned into the primary sensory centers, the subesophageal ganglion, and the central brain), 2) thoracic (usually three separate segments), and 3) abdominal (the segmented quantity

varies by species) (Borst, 2009; Clandinin & Zipursky, 2002). Specifically visual ganglia in insect nervous systems form three layers: ‘lamina, medulla, and ‘Lobular complex’ (Borst, 2009; Clandinin & Zipursky, 2002), see Figure 2.

In *Drosophila* specifically the abdominal ganglia and the three standard thoracic ganglia are fused into a combined thoracic ganglion. This thoracic ganglia is connected to the head ganglia via a ‘cervical connective’ made up of approximately 3600 axons of the combined acceding and descending neurons (Borst, 2009; Clandinin & Zipursky, 2002; Mast, et al., 2006; Pecot, et al., 2014; Sato, Suzuki, & Nakai, 2013; Ting & Lee, 2007; Velez & Clandinin, 2008). As with all insect systems there are three visual layers formed by ganglia into regions; lamina, medulla, and lobular complex- which in dipteran flies is two layers, the lobula and the lobula plate (Borst, 2009), another level to the visual processing is the compound eye or retina (Sanes & Zipursky 2010). Additionally there are two chiasms, one between the medulla and lamina, and the other between the lobula complex and the medulla (Borst, 2009; Clandinin & Zipursky, 2002).

The retina of *Drosophila* are represented by roughly 750 ommatidia units that contain the eight photoreceptor cells (Sanes & Zipursky, 2010; Sato, Suzuki, & Nakai, 2013; Wernet & Desplan, 2004) The lamina of *Drosophila* have approximately 6000 cells, which combine to roughly 13 cell types (L1 - L5 laminar monopolar cells, 1 to 2 amacrine cells, 3 medulla neurons (C2, C3, & T1), and three glial cells), and contain 750 units called cartridges of specific cell types (11 classes of neurons per cartridge) and connections (Behnia & Desplan, 2015; Belusic, 2011; Morante & Desplan, 2004; Paulk , Millard & van Swinderen, 2013; Sanes & Zipursky, 2010; Sato, Suzuki, & Nakai, 2013; Ting & Lee, 2007; Velez & Clandinin, 2008; Wernet & Desplan, 2004). The medulla is

more complex and dense, with 40,000 cells represented by 70 cell types that can be divided in three major layers, and each cell type is confined to units known as columns (Behnia & Desplan, 2015; Belusic, 2011; Morante & Desplan, 2004; Sanes & Zipursky, 2010; Sato, Suzuki, & Nakai, 2013; Ting & Lee, 2007; Velez & Clandinin, 2008; Wernet & Desplan, 2004). The lobular complex contains approximately 15,000 neurons, a majority are large neurons of the vertical or horizontal systems (Morante & Desplan, 2004; Ting & Lee, 2007; Velez & Clandinin, 2008), the lobula is theorized to specifically process color vision, polarized light vision, and spectral preferences (Behnia & Desplan, 2015; Belusic, 2011), and the lobular plate is theorized to process motion detection vision (Behnia & Desplan, 2015; Belusic, 2011).

The *Drosophila* eyes use isolated units of ommatidium, which is described as the functional retinal unit containing eight photoreceptors and their neurons (retinula cells- or R-cells). The R1, R2, R3, R4, R5, and R6 (R1-R6) photoreceptors express the same opsin gene, and are associated with the achromatic and motion detection channels, which can be combined to the achromatic motion channel (like rods in vertebrates). The R7 and R8 photoreceptors express UV- and blue-green sensitive opsins (respectively), which could be thought of as the cones in flies (Rister, et al., 2007; Sanes & Zipursky, 2010; Ting & Lee, 2007; Velez & Clandinin, 2008). A negative feedback loop of intracellular synapses between the photoreceptors and the monopolar cells in the lamina of *Drosophila* regulate responses. Specifically the negative feedback loop affects photoreceptor responses by controlling the speed, amplitude and quality of the signals being transmitted (Zheng, et al., 2006).

The developed lamina, with axonal growth and termination of the R1-R6 photoreceptor neurons in the structure directly beneath them, is considered to be the first level where visual information is integrated by neuronal synapses, also called the first optic ganglia (Behnia & Desplan, 2015; Beluisic, 2011; Borst, 2009; Clandinin & Zipursky, 2002; Janssen, Budd & Damen, 2011; Mast, et al., 2006, Morante & Desplan, 2004; Paulk, Millard & van Swinderen, 2013; Pecot, et al., 2014; Rister, et al., 2007; Sanes & Zipursky, 2010; Ting & Lee, 2007; Velez & Clandinin, 2008). During eye morphogenesis, the R1-R6 photoreceptor neurons are matched to the target layer by anterograde signals that control neuronal differentiation and target proliferation, additional signals (axon-derived) couple layer specificity with target survival in the *Drosophila* Visual System: N-cadherin is expressed by both the lamina and photoreceptors to produce high synapse quality in the lamina core (Schwabe, et al., 2014). The R1-R6 axons produce a protein Jelly Belly (*Jeb*), which interacts with a receptor (anaplastic lymphoma kinase- *Alk*) found on the dendrites of a lamina monopolar cell (L3). This *Jeb-Alk* interaction controls the L3 neuron survival, and due to the *Jeb-Alk* interaction, the L3 axons then produce Netrin, which is another layer targeting specific signal that regulates a different neuron in the lamina, causing the 'lamina furrow' (Janssen , Budd & Damen, 2011; Pecot, et al., 2014; Sato, Suzuki, & Nakai, 2013; Wernet & Desplan, 2004). The lamina has three major cell types, the monopolar neuron cells (five subtypes called L1, L2, L3, L4, and L5, or L1-L5), the wide field neurons (three classes, including amacrine cells), and the centrifugal cell fibers from the medulla (T1, C1, and C2) (Borst, 2009; Clandinin & Zipursky, 2002; Mast, et al., 2006; Morante & Desplan, 2004; Sanes & Zipursky, 2010; Ting & Lee, 2007; Velez & Clandinin, 2008).

The units of the lamina are determined by the synapse of the L1-L3 neurons with the axons of the R1-R6 in a cartridge, each cartridge receives inputs from the R1-R6 cell types, but only the combined R cells that see the same point in space. Since the fly eye is convex, and each of the eight photoreceptors in each ommatidium 'see' different points on the visual axes, the six ommatidium that are next to each other (neighbors) have a different R cell that projects to the same cartridge in the lamina; the R1 of the first ommatidium, the R2 of the next, the R3 of the next, etc, each 'see' the same pint in space, so contain the comprehensive information of the same point, each by a different photoreceptor, but the same type- this is also called neuronal superposition (Behnia & Desplan, 2015; Beluisic, 2011; Borst, 2009; Clandinin & Zipursky, 2002; Mast, et al., 2006, Morante & Desplan, 2004; Sanes & Zipursky, 2010; Takamura, et al., 2011; Ting & Lee, 2007; Velez & Clandinin, 2008).

Once the photoreceptors R1-R6 create (tetrad) synapses in the lamina to four parallel pathways, or postsynaptic elements (PSE) (Morante & Desplan, 2004; Rister, et al., 2007; Sanes & Zipursky, 2010; Wernitznig, et al., 2015). These PSEs are the three monopolar cells (L1-L3) and an amacrine cell derived pathway (*amc/T1*). The most prominent connections are the L1 and L2 monopolar pathways that are almost invariant and are sufficient (and necessary) for motion-dependent behavior in *Drosophila*. The interaction between L1 and L2 will be dependent on the contrast in the level of responses to different stimuli between the two pathways. If there is a high contrast, then L1 and L2 are redundant and either one will be sufficient, while at intermediate contrast levels the L1 pathway mediates a back-to-front polarity motion, and L2 mediates the inverse of L1 (the front-to-back polarity motion), at this intermediate level the amc/T1 pathway

enhances the L1 pathway. Finally in low contrast levels the two pathways (L1 and L2) are directly dependent on each other to preform motor processing. The L3 monopolar pathway does not assist the L1 or L2 pathways and has been studies for its contribution to orientation-dependent behaviors, not motion detection (Borst, 2009; Clandinin & Zipursky, 2002; Mast, et al., 2006, Morante & Desplan, 2004; Rister, et al., 2007; Sanes & Zipursky, 2010; Takamura, et al., 2011; Ting & Lee, 2007; Velez & Clandinin, 2008). Another lamina cell type (L4) is also proposed to match with the L2 synaptic outputs directly to a transmedulla target neuron for front-to-back motion detection- the L2/L4/Tm2 circuit pathway (Takamura, et al., 2011).

Each lamina pathway will transmit axons to discrete columns within the ten layers of the medulla (M1 - M10), and the central photoreceptor cell (R7 and R8) neurons bypass the lamina to terminate in the medulla (R7 terminates in the "M6" and R8 in the "M3" layers) (Behnia & Desplan, 2015; Beluisic, 2011; Borst, 2009; Clandinin & Zipursky, 2002; Mast, et al., 2006, Morante & Desplan, 2004; Sanes & Zipursky, 2010; Sato, Suzuki, & Nakai, 2013; Takamura, et al., 2011; Ting & Lee, 2007; Velez & Clandinin, 2008; Wernet & Desplan, 2004). In addition to the R7 and R8 terminal synapses, the outer six layers (M1-M6) contain the synapses of the L1-L5 monopolar pathways, which could synapse on multiple layers of the medulla, but all the axons synapse on an interneuron or a transmedulla (Tm) neuron (this synapse is a medulla column). The Tm1 and Tm2 receive information from the L2 pathway, and (as discussed above) the L4 also connects with the Tm2 if the L2 pathway is synapsed to it (Takamura, et al., 2011). Tm neurons connect one or more layers of the medulla to the lobula, a subtype of transmedulla neurons projects to the entire lobular complex (TmY), combined

with medulla intrinsic neurons (wide field neurons, distal medulla intrinsic neurons), and Bushy T cells (T2 and T3) also project to the lobula but the bushy T4 cells are exclusive to the lobula plate (Borst, 2009; Clandinin & Zipursky, 2002; Mast, et al., 2006, Morante & Desplan, 2004; Sanes & Zipursky, 2010; Ting & Lee, 2007; Velez & Clandinin, 2008).

The lobula complex processes all the information about the visual world that the neuronal system has compiled into distinguishable features. For example the R7 layer M6 expressly produce distal medulla intrinsic neuron 8 (DM8), which mediates UV-sensitivity by projecting to T5 neurons, and transmitting to lobula layer 5. The Bushy T5 cells are the only known cells that connect the two parts of the lobular complex together. And while the lamina and medulla neurons have smaller diameters, the neuronal cells found in the lobular plate are tangential cells compared to branching trees. The most studied of these lobula plate tangential cells are the Horizontal system (HS) and the Vertical System (VS) motion cells. For an idea of how large these neurons are; six VS cells can cover *Drosophila*'s visual field with overlapping dendritic fields, connected via gap junctions (Borst, 2009; Clandinin, & Zipursky, 2002; Mast, et al., 2006, Morante & Desplan, 2004; Sanes & Zipursky, 2010; Ting & Lee, 2007; Velez & Clandinin, 2008). Which processes the motion detection features into behaviors if applicable.

Given this, there is some structural similarities between *Drosophila* and vertebrates. Such as their being a small number of major classes of neuronal cells (six in *Drosophila*, five in vertebrates), there are multiple cellular layers of the neurons on which the arrangement of the neurons is predictable and regular, the transition between each level is orderly, involving very specific integration and convergence patterns on neuronal arrays, and parallel sub-lamina formed from the synaptic segregation of specific

subtypes. And these structural similarities can then be compounded with visual function produce common design principle between the two systems: there is hierarchical processing that are mediated by convergence and lateral interaction, and parallel processing is mediated by the layered connections (Sanes & Zipursky, 2010).

5.0. Color Vision

Color vision has been hinted at in other sections of this chapter, but never fully explained. Color vision is complicated, but also has many conflicting sides that researchers have created for themselves. How loose or harsh color and color vision is defined and expressed in species can directly influence the number of species that have color vision. A strict definition would exclude all species except Humans, and too loose a definition and then some bacteria would be classified as having color vision. So let's decide on some key structures and systems that would create a comprehensive definition of what color vision is.

5.1. Defining color vision.

When receiving signals from the opsin proteins the receptors transmit contrasting information along the same pathways. The key aspect of color vision is the ability to have both the neural framework and the receptors for detecting different wavelengths. This dependence on the number of photoreceptors dedicated to color and complexity of the channels they are interpreted with, can determine how much contrast and information is gained (Cronin, et al., 2014). The sensitivity of a photoreceptor can determine how few wavelengths it can be activated by, or how many. Intensity and saturation matter, and the

ability to discriminate colors without those two qualities affecting wavelength determinations is dependent on the number of photoreceptors for color vision there are. As Intensity can be the excitability of the photoreceptor, or the brightness of the wavelength, with no effect on the wavelength itself. Saturation is quality of the hue of color, or whether grey/muddiness of the hue matters, as this should not determine how a color is 'named' by the visual system- blue is blue no matter if a car hasn't been washed in a while.

Color vision, in short, is when a species has two or more receptors that are sensitive to different wavelengths, and the neural systems to interpret the data obtained from the receptors (Briscoe & Chittka, 2001; Desplan, 2004; Goldsmith, 1990; Kelber & Henze, 2013; Skorupski & Chittka, 2011). Pichard, Briscoe & Desplan (1999) attempted to specify that color vision must also include the ability to discriminate between wavelengths of color without intensity being a factor. The simplest issue with any definition of a concept, is that it is hard to define in context- what is color? - When does color vision evolve? - Is there a set moment when color vision begins? (Land & Nilsson, 2012).

Unlike in other senses, color is based on how much a photoreceptor is stimulated in contrast to a second photoreceptor with a sensitivity slightly opponent to the first. This is antagonistic color processing, which determines stimulation based on opponent neural pathways. Simplified "is this more one color than the other?" (Chatterjee & Calloway, 2003; Chichilnisky & Wandell, 1999). In most pathways (and is true in humans), "more blue not yellow, or more red not green".

However the ability to determine wavelengths of color and discriminate between them is something that has been produced in computer systems (Moreno, Grana, & d'Anjou, 2010; Swain & Ballard, 1991), and shown to exist in some plants (Skorupski & Chittka, 2011).

The determination of wavelengths by photoreceptors is always described within the sensory system of vision, and the sensory system is defined with some type of visual organ- an eye, usually two eyes. And then there is the processing of the information obtained when discriminating the wavelengths of light. So then a neural network of some complexity would be necessary for the discrimination of wavelengths.

So color vision is the discrimination of wavelengths by more than one photoreceptor, which are localized in a visual organ, and processed by a neural network. And color vision can only be possible with two or more photoreceptors, and processed by a neural network.

5.2. Diversity of color vision.

Multiple visual pigments are needed to form color vision, all eyes collect and absorb light. Hering, et al. (2012) argues the velvet worm as the LCA of arthropod color vision, and that color vision evolved with the evolution of compound eyes in arthropods. As indicated above, increasingly complex tasks in visual behavior would drive the evolutionary complexity (Land & Nilsson, 2012). In the case of detecting light intensity and movement, only one type of photoreceptor is necessary, while color vision requires two or more types of photoreceptors. In terms of prey (or predator) detection (Endler, 1991; Houde, 1997), the movement of an object can take precedence over what color the

object is (Melin, et al., 2006), whereas determining fruit ripeness is necessary for survival purposes and would require two or more photoreceptor types. Each is a complex component of vision, but requires different levels of functional mechanisms and bias to function. Further complication arises when two signals are received along the same pathway. The innate bias of reception of color over movement, or vice versa, is dependent on the evolutionary history of the population.

A major assumption of color vision is that it decreases in quality/ability as night vision (rod-predominate achromatic processing in vertebrates) is needed, or that night or low light vision cannot process color readily if at all because, at least in vertebrate vision, rods do not activate or process wavelength differences (therefore color differences) (Gehring, 2014; Yamaguchi, et al., 2008). This is not absolute, but a commonly determined rule in vision, a major exception being a study performed by Land & Osorio (2003), which described how the elephant hawk moth uses starlight, and can use its trichromacy color vision profile to find flowers at night.

Color vision is a highly variable system, that can add spectral sensitivities for information, gathering and refining absolute sensitivity peaks, and some species have unique systems of color vision mechanisms, inference, or filtering processes (Osorio & Vorobyev, 2005).

5.2.1. Between & within species.

There is a wide range of color vision variation between humans and mantis shrimp, or spiders, or any number of visual sensory systems that is present in the world. With humans, in an oversimplified sentence, a trichromatic system of opponent

processing can discriminate between long-wavelength sensitive (LWS), middle-wavelength sensitive (MWS), and short-wavelength sensitive (SWS) stimuli through the three corresponding photoreceptors (cones) that are tuned to these three spectral peaks, with a rod photoreceptor for achromatic discrimination (Deeb & Motulsky, 1996; Dulia, et al., 1999: Imamoto & Shichida, 2014; Johnston, Esposti & Lagnado, 2012; Nathans, et al., 1986; Neitz & Neitz, 2008; Neitz & Neitz, 2011; Rushton, 1972; Shichida & Matsuyama, 2009). Humans are not the only trichromats, and are not the only species to use opponent processing for discrimination. A majority of color vision systems were determined through conditioning procedures and behavioral observations (Kelber, Vorobyev & Osorio, 2003; Vorobyev & Osorio, 1998; Yamaguchi, et al., 2008).

The necessary systems that must be in place for evolution to occur is genetic variability of traits within species. So it is not surprising when population species samples are assayed for spectral sensitivity, that variations between populations of species dose exist- primates, guppies and bees have some variable expression (Briscoe & Chittka, 2001).

In some new world monkeys (NWM) there are three LWS opsins that can be expressed, each with a slight variation in spectral sensitivities, and all three regularly are present in a population (Melin, et al., 2006; Surridge, Osorio, & Mundy, 2003). Humans have variations in color vision, though the most readily understood is the defective trichromatic wherein (usually the LWS or MWS) one of the X-chromosome linked opsin genes is lost, which does produce a variation in color vision within a species (Deeb & Motulsky, 1996; Nathans, et al., 1986; Rushton, 1972), but amino acid substitutions in the LWS or MWS opsins can produce spectral peak shifts of 1nm, 5nm, or more,

dependent on the amino acid substitution and where within the opsin (Neitz & Neitz, 2011).

Mice have been shown to use cones for achromatic processed, with the use of achromatic-contrast-selective channels and receptors (calcium light driven) in tandem with the standard dichromatic color vision process system, and rod-achromatic system (Baden, et al., 2013b).

The Hofmann, et al., (2009) paper is particularly robust in the discussion of between-species variation, and gives distinct evolutionary time frames in addition to an expressed ecological biases for opsin expression and duplications. Using in total 65 different *cichlid* species from two different lakes. And Frentiu, et al., (2007b) condenses known opsin gene expression in a variety of Butterfly geneses and species, which are theorized to have formed through gene duplication events. Other papers expressly discuss specific species and the conditioning experiments that indicate true color vision profiles (Behnia & Desplan, 2015; Blackiston, Briscoe & Weiss, 2011; Borst, 2009; Bowmaker, 2008; Briscoe, 1998; Briscoe & Chittka, 2001; Chittka, et al., 2014; Collin, et al., 2004; Deeb & Motulsky, 1996; Desplan, 2004; Dulia, et al., 1999; Fischbach, 1979; Frentiu, 2007a; Giurfa, 2004; Gumbert, 2000; Hernandez de Salomon & Spatz, 1983; Imamoto & Shichida, 2014; Kelber & Pfaff, 1999; Kinoshita, Shimada, & Arikawa, 1999; Koyangi, et al., 2008; Lotto & Chittka, 2005; Marshall & Arikawa, 2014; Menne & Spatz, 1977; Neitz & Neitz, 2008; Neitz & Neitz, 2011; Ogawa, et al., 2012; Osario & Vorobyev, 2008; Paulk, Millard & van Swinderen, 2013; Pichard, Briscoe & Desplan, 1999; Sison-Mangus, et al., 2006; Surridge, Osorio, & Mundy, 2003; Tang & Guo, 2001; Vorobyev, et al., 2001; Wakakuwa, et al., 2010; Yamaguchi, Desplan, & Heisenberg, 2010; Yuan, et

al., 2010; Zaccardi, et al., 2006). Though each of these papers can sometimes indicate that the source of light can sometimes affect processing components of the color vision neural pathways.

5.2.2. Between genders.

Sometimes the expressed opsin/visual pigments can be dependent based on gender within a species, and can be considered distinct from simple variations in color vision and photoreceptor profiles within a species. And while some papers were discussed in the context of species variation (Melin, et al., 2006; Nathans, et al., 1986; Rushton, 1972); but it is much more complex. Sex/gender dimorphisms in species are more readily explained by sexually selective evolution (see section *3.1.3. Sexual selection* above) on visually conspicuous colors displayed on males of a species. It can be implied then that females should be able to react to the color pallets expressed by the males, and then there may be a visually dimorphic opsin-expression to discriminate those sexual selective colors. This is not a hypothesis that is discussed in sexually dimorphic vision papers, and may yet be hard to tests in behavioral simulations. However, there are papers that discuss the expression-profiles of opsins as being sexually linked.

Drosophila species (three in total) were studied based on the opsin-expressions and region-distribution of the ommatidium types. While the frequency of DRA, and pale and yellow ommatidium types were variable across all studied species and strains, females of all species were determined to have more ‘pale’ and *Rh3*-expressing ommatidium than their corresponding males in the species/strain (Hilbrant, et al., 2014). *Colias erate* (butterfly) determined that while the opsins expressed in photoreceptors

were not variant based on gender, the spectral sensitivity of the photoreceptors was variant between species due to florescent pigment distribution to create spectral sensitivity shifts; so the blue-sensitive receptor in males was violet-sensitive in females (Ogawa, et al., 2012).

New world monkeys, such as the *Capucinus*, have three variants of the LWS opsins that are expressed on the X-chromosome. And depending on the sexual paring, the different spectral sensitivities could be expressed in six genotypic systems (Bowmaker, 2008; Melin, et al., 2006; Neitz & Neitz, 2011; Surridge, Osorio, & Mundy, 2003). Though Melin, et al., (2006) describes how the variations in the sensitivity peaks of the three LWS opsins can determine the preferred ripeness of food that the *Capucinus* hunt for, the males that are deficient in trichromacy are shown to be more successful in finding insects (probably by movement) under leaves than their trichromatic-females.

A less studied model was determined through human color vision deficiencies, which are more common in males, though not exclusive. These deficient males and females usually have a MWS or LWS deletion (Nathans, et al., 1986; Rushton, 1972; Surridge, Osorio, & Mundy, 2003) or other recombinant X-chromosome issue, and as males only have one X-chromosome any deletion is more likely to express in males, whereas females would need two X-chromosomes that are deficient in either the LWS or MWS opsin gene on both chromosomes, though there are sensitivity variations within the species. Jordan, et al., (2010) describes how these X-linked deficiencies could select for a second duplication event on the opsin-deficient-X-chromosomes. While a majority of the participants did not express a unique spectral peak in the LWS or MWS variations, one female did show a third sensitivity peak, while a separate LWS, MWS, and SWS peaks

were also recorded. This fourth cone peak sensitivity, a tetrachromat, is hypothesized to be expressed in females only.

5.3. Color vision in context.

Earlier, when describing different types of opsin genes, there were opsins described that did not have a direct and obvious role in vision, but still retained light sensitive receptors. Given the color vision definition above, could a fungus be classified as having vision if its opsin is used to determine light from shade? If two distinct receptors were detected could color vision be hypothesized? Plants have been documented to avoid shade growth by using two red-light receptors, and some machines have been developed to sort food on the basis of color (Skorupski & Chittka, 2011). And foraging conditions in some experiments show preferences for color but not constancy (Pohl, Van Wyk, & Campbell, 2011).

On the reverse side: there have been humans who have lost color vision, but can still discriminate color by wavelength (Douglas & Jeffery, 2014; Skorupski & Chittka, 2011). Could this be defined as color vision?

These hypothetical questions can be answered in a lab if context and personal/evolutionary history are taken into account. In the grand scheme of these questions, we can discard plants and machines as having color vision- even if the argument is valid-as plants and machines do not have distinct and discernable visual organs that are an assumed first component of color vision. How can color vision be determined, and what limits are inherent in color vision? In the definition above, the ability to interpret the data the receptors have obtained from wavelengths of light is

necessary for color vision. The data received could be directional, intensity, hue, polarization of wavelength, which a receptor can be sensitive to, and determine changes in the baseline set; in other words the collective components of a light signal and the collective components of the light-receptor determine the quantity and quality of the data obtained. This sensitivity to changes is wavelength discrimination (Hsu & Yang, 2012; Hurlbert, 1996; Schnaitmann, et al., 2013; Skorupski & Chittka, 2011).

In some papers there are "grades" of color vision given when behavior is expressed (Kelber & Osario, 2010; Kelber, Vorobyev & Osorio, 2003; Maximov, 2000) these are classified by: 1) color taxes or light environment seeking, 2) wavelength-specific behavior directed toward objects, 3) color learning through neural representation of color, 4) color appearance, including characterization. Each receptor is spectral sensitive to a wavelength, which is well spaced from the other receptors.

Wavelength discrimination is based on the premises that two photoreceptors are present and have overlapping sensitive scales. This allows for wavelengths of color to excite by differing amounts, two distinct receptors, which are then interpreted by the degree of sensitivity and activation. This processing by comparing activations is called "opponent processing" (Skorupski & Chittka, 2011). The distinction is key to determining how individuals with acquired color-blindness can still discriminate by wavelength when tested. However, wavelength discrimination is a facet of color vision, and discrimination by wavelength does not represent color vision outright, yet color vision cannot exist in a species without discrimination.

6.0. Forward

Given the predominance of color vision to arise for ecological reasons, selective reasons, because of biases, or from duplication events and spectral tuning, it is not surprising that color vision is being discovered in more species the more studies are done. There has been a slight connection between the predominance of color vision and cognitive abilities, as the use of more than one photoreceptor is required for color vison, it also significantly benefits the species to gain that extra information to increase fitness. Though further studies are needed. And cognitive evolution is not an assured end result of color vision, or vision at all. Consider that the Dinosaurs and their predecessors evolved variations of the eye for over 165 million years, the cognitive abilities- and implied intellectual developments, never arose. Yet in the total evolutionary history of our own species, which dates back to a maximum of two million years, did develop these cognitive abilities in a very short time (Nat Geo Evolution, 2016). That cognitive connection should be further studied.

Despite the uninvestigated holes in visual sensory development, neural; circuitry, and evolutionary models, there is a lot of information that has been empirically studied for vision. And the use of that information in studying ecological systems, and specie's interactions with ecological models could flesh out the missing information later.

Chapter 2: An Experimental Evolution Study on Color Vision in *Drosophila melanogaster*

1.0. Introduction

Experimental evolution studies, as discussed in Chapter 1 (Endler, 1986; Fox & Lenski, 2015; Garland & Adolph, 1994; Gould, 1990; Kawecki, et al., 2012; Pennisi, 2013), are typically difficult to perform given the sheer timeframe that an experiment must be performed under, and the species to experiment on must be selected carefully (Kawecki, et al., 2012). In this experimental evolution study, *Drosophila melanogaster* is our model species, and individual lines were selectively pressured to evolve hue preferences across 22 generations. These lines were randomized into three treatment groups and two separate control conditions; each of the treatments and each of the controls had 12 replicates, for a total of 60 different evolving population lines.

Drosophila melanogaster was chosen to be the studied population for a number of reasons. The color vision system of *Drosophila melanogaster* is well studied and documented (Erclik, et al., 2009; Gonzalez-Bellido, Wardill, & Juusola, 2011; Harzsch, Melzer & Muller, 2007). A variety of conditioned discrimination studies have been performed for *Drosophila melanogaster* and other *Drosophila* species, with regards to oviposition and the corresponding behaviors (Allemand & Bouletreau-Merle, 1989; del Solar & Palomino, 1966; Hernadez de Salmon & Spatz, 1983; Joseph, et al., 2009; Manjunatha, Dass, & Sharma, 2008; Markow, Beall, & Matzkin, 2009; Menne & Spatz, 1977; Ohnishi, 1977; Rockwell & Grossfield, 1978; Ruiz-Dubrevil, Burnet, & Connolly, 1994; Takemura & Fuyama, 1980). And they were in readily aviable supply in the research lab.

In some more recent studies of *Drosophila melanogaster* behavior (usually larval wandering) is studied (de Belle, Hilliker & Sokolowski 1989; Riedl, et al., 2007;

Schwartz, et al., 2012) genetically, or some other species is studied with respect to light and mating /oviposition behavior (Zhang, et al., 2010). When oviposition are documented for *Drosophila melanogaster* and other *Drosophila* species, the substrate quality is being assessed, how retention /egg size /embryonic development vary between species and if they affect oviposition rates (Abed-Vieillard, et al., 2013; Allemand & Bouletreau-Merle, 1989; del Solar & Palomino, 1966; Markow, Beall, & Matzkin, 2009; Ruiz-Dubrevil, Burnet, & Connolly, 1994; Yang, et al., 2008), and if oviposition is studied under a sensory system it is usually olfactory preferences on substrates (Dweck et al 2013; Mery & Kawecki 2004a; Mery & Kawecki 2004b; Dunlap & Stephens 2009), although enhanced color learning has been shown to evolve under certain conditions (Dunlap & Stephens 2014).

If oviposition behavior has been studied under light environments for *Drosophila melanogaster*, then it is a short term study for patterning of constant day, or day-night cyclic systems (Ohnishi, 1977). Hernandez de Salmon & Spatz (1983) determined two optima peaks for *Drosophila melanogaster* wavelength discrimination at 420 nm and 495 nm. Salcedo, et al., (1999) determined peak absorptions in the UV, at 475 nm and 515 nm.

Washington (2010) built upon previous work to determine photo-tactic color vison in *Drosophila melanogaster.* And while conditioning experiments for *Drosophila melanogaster* to determine color vision (Hernadez de Salmon & Spatz, 1983; Menne & Spatz, 1977; Rockwell & Grossfield, 1978; Washington, 2010) are readily available, they are not experimental evolution studies. Additionally, most light behavior studies directly

involved with *Drosophila melanogaster*, were performed in the 1970s to 1980s, and were usually preformed with flight simulators and beams of light.

Oviposition behavior is key, as the only parental investment that *Drosophila melanogaster* makes is where their eggs are laid, and the direct choice behavior can be determined by egg laying. In this study, I used the techniques of experimental evolution to test how female color preference for the substrates where they oviposit may evolve under different choice contexts. By manipulating the choices females were given intensive, one directional selection was induced to produce a hypothesized fast experimental evolution study where the choices made by females could be determined in a repeatable way. Eggs were quantified in this experiment to determine preferences over time and under selective pressure.

2.0. Methods

2.1. Experimental design & stimuli.

Disks of hues were produced from previously determined spectrally sensitive wavelengths of *Drosophila melanogaster* (Hernandez de Salmon & Spatz, 1983; Salcedo, et al., 1999; Washington, 2010), and were converted to a Red-Green-Blue (RGB) hexadecimal input so the wavelengths- now hues, could be printed into re-useable disks via a color laser-printer. These wavelengths were converted on the websites: www.teachersdomain.org/asset/1sps07_int_wavelength/ and https://academo.org/demos/wavelength-to-colour-relationship/ where Wavelengths from 385 nm to 565 nm were charted in RGB Hexadecimals. See Table 1, which shows the hues used in the experiments.

At the onset of the experimental evolution study, it was determined that there would be three different selection treatments, and two different controls, for a total of five line designations. Each line designation would have 12 replicates, for a combined total of 60 experimental lines. These line designation were used as a short-hand code representing the selection treatment, or no-treatment, and the replicate within that treatment (no-treatment).

2.1.1. Line designations & treatments.

Initially, wild population eggs were collected in 250 mL milk bottles containing 50 mL standard fly food in a field in 2012 at Fenn Valley, Michigan. For a year, each generation was inspected to weed out other bugs. The wild lines were then maintained until they were collected for my experiment on 7/8/2014.

The Fenn Valley population (FV) was maintained with twenty milk bottles of fly food, with 500 eggs each, which were reared each generation at 18 °C, for 19 days. When flies emerged, the bottles were placed in a closed population cage and given 3 standard Petri-dishes (10 cm in diameter) filled with 50 mL of standard "Fly Food" each day, for 3 days. (Recipe for "Fly Food" is documented in Appendix 2).

For my experiment three-hundred sixty vials, containing eighty eggs each, were collected from the wild population on 7/8/2014. The vials were randomly ordered, then grouped into sixty lines with six vials each, collectively known as the "Fenn Valley" population.

Each Line was assigned a number from 1 to 12, and assigned a letter designation A, B, or C; the remaining lines were designated Controls 1 through Control 24, the letter

designation (A, B, or C) determined the Experimental Evolution Treatment Type the lines would be selected under. These Treatment Types and Controls are documented in Figure 6.

The controls still had to be randomized because Control 1 through Control 12 were given color choices similar to the C- Line Treatment Types, but no selective pressure was induced. Control 13 through Control 24 were given Fly Food, so that a second control set, where no color hues were introduced during the selective generations, could exist.

The lines were reared at 24 °C for 10 days (after spending 12 hours at 14 °C). Each line was introduced into separate cages with two Petri dishes with 50 mL of standard lab Fly Food. The cages were put into a Climate Chamber set at 24 °C, under Hitlights© controlled LEDs set to cool white for three days, undisturbed. See Figure 7 for fly cage drawings with the Hitlights LED strips.

For the A Lines (Selection toward a Higher Hue) each generation was given a slide of two blue (“B” disks) and two aqua (“A” disks) hues. As shown in Figure 8A, where the 1, 2, 3, and 4 are representing a location where the color disk hue and agar plate will go.

a. Agar food recipe is outlined in Appendix 2. For Shorthand this combined recipe will be called just “Agar”.
b. There are four patterns that the A- Lines two hues can be randomized into that were used, which are depicted in Figure 8B, 8C, 8D, and 8E. Each succeeding generation was cycled through the different patterns.

For the B Lines (Selection towards Lower Hue) the same setup as the A Lines were tested under remained the same, with the hue disks changing slightly, with the Green hue

disks (abbreviated to “G”) replacing the “B” disks, and Figure 9 illustrating the four pattern combinations, which was designated the same way as the A Lines.

For the C Lines (Selection towards Middle Hue) each generation is given a slide of two B disks, two A disks, and two G disks. The combinations were presented in six patterns that were used illustrated in Figure 10. Each line was randomly assigned, via computer, which pattern would be presented at generation 1, and each generation thereafter was cycled through the five other combinations, then starting the cycle over until the experiment ended.

For the lines designated as Control 01 through Control 12, called the the Color Controls collectively, each generation is given a slide of two B disks, two A disks, and two G disks. The combinations were presented in six patterns that were used illustrated in Figure 10. Each line was randomly assigned, via computer, which pattern would be presented at generation 1, and each generation thereafter was cycled through the five other combinations, just like the C Lines. Then for the lines designated as Control 13 through Control 24, which were also called the Food Controls, each generation would be given one standard Petri-dish with 50 mL of Fly Food.

Before the first generation had matured, 700 mini Petri-dishes (4 cm in diameter) were labeled in red sharpie along the height edge of the dish so as not to create shadow void patterns on the Hue disks. The plates were labeled numerically from 0001 to 0700. Every generation used 240 mini Petri-dishes (also called Agar plates) were filled with 1.5 mL Agar solution. Each mini Petri-dish was compositionally the same, and then each plate was recorded on the pre-prepared data sheet to designate which line, position, and

hue disk the agar plate rested on. See Appendix 2 for the Agar recipe, see Appendix 3 for sample Data Sheets.

Each line was given as long as necessary to lay enough eggs on the proper hue to propagate the next generation, this time frame was altered within the first five generations due to an unforeseen experimental flaw. For the first four/five generations this time was 1.5 hours, the following generations were approximately 3 hours, due to the Lines laying less than the needed 480 eggs to perpetuate the next generations during the first five generations because of this time constraint. Despite this alteration, each data sheet records the start time and end time of the trial, as well as any notable occurances during the day- weather, construction, blackouts, etc.

After a generational selection treatment had occurred, the slides were pulled from the cages, and they were photographed in any order, separate from the hue disks, and only photographed with Agar plates from the same cage. See Figure 11 to see a demonstration of the photographed plates. The position of the photographed plate does not correlate to the location of the same agar plate in the cage during the trial. The plate location in the photograph was recorded in a separate lab book from the Data Tables where the hue disk and location in the cage were recorded. See examples of this in Appendix 3.

After the photographs were taken in .RAW on a camera, they were downloaded to an external hard-drive and converted from .RAW to 16 bit .TIFF, and relabeled from the standard photograph number to sW_gY_x00ZZ format; sW: represents the generation (or selection) the plate was used in (W), E.g.: s1, s2, s3, s20. gY: denotes the group (or day of the week the trial was conducted). Since there are sixty lines, four of each of the A-Lines, B-Lines, C-Lines, Color Controls, and Food Controls were run on a Tuesday, the

next four of each set were run on a Wednesday, and the last four of each set were run on a Thursday, for the sake of sanity. The cages that were run on a Tuesday were denoted g1, Wednesday was g2, and Thursday was g3. x00ZZ: the photograph number in relation to the first two parts of the photograph labels. Photograph s1_g1_x0001= photograph number 1 of selection/generation 1, in group 1.

When the photographs have been taken, the eggs from specific agar plates are used to rear the next generation as described in Figure 6. A- Lines (using the hue disk and location data sheets) are reared from eggs, removed from plates that were run on Aqua hue disks. Each Line gets 80 eggs per vial, at six vials per line (i.e. 480 eggs per line). B- Lines (using the hue disk and location data sheets) are reared from eggs, removed from plates that were run on Aqua hue disks. Each Line gets 80 eggs per vial, at six vials per line (i.e. 480 eggs per line). C- Lines (using the hue disk and location data sheets) are reared from eggs, removed from plates that were run on Aqua hue disks. Each Line gets 80 eggs per vial, at six vials per line (i.e. 480 eggs per line). Control Lines 1 through 12 (also called Color Controls), are reared from eggs removed from all agar plates equally. This is either 80 eggs per plate to prevent drift based on location, or 160 eggs (or two vials) per hue disk, to minimize selective pressure towards or away from any hue. Control Lines 13 through 24 (also called Food Controls) are reared from eggs removed from Fly Food only. This is to determine if there is a natural drift towards or away from any hue in this experiment, and compare the end results against a isolated control group.

Each generation was reared at 24 °C for 10 days after spending 12 hours at 14 °C. Hatched flies are knocked into clear cages with two petri dishes with 50 mL of Fly Food for three days, as shown in Figure 7.

2.1.2. General assay procedure.

Testing, rearing, and selecting on each line was repeated for the next 20 generations of selection. After the selection/generation 21 trials, a new Fly Food petri dish with 50 mL of Fly Food were given to the A- Lines 1, 5, and 9; B-Lines 1, 5, and 9; C-Lines 1, 5, and 9; Control Lines 1, 5, and 9; and Control Lines 13, 17, and 21. The Lines were left alone for 12 hours to lay eggs on the new food. After the 12 hours, nine additional replicates of the A-lines and B-lines were collected, and twelve additional replicates of the C- Lines and Controls were collected.

After the selection/generation 22 runs normally with agar (alongside the replicates collected after generation 21), repeat what happened after generation 21 above, using the numerical lines 2, 6, and 10, as well as Control 14, 18, and 22. After generation 23 numerical lines 3, 7, and 11, as well as Control 15, 19, and 23 were collected following the same methods. After generation 24 numerical lines 4, 8, and 12, as well as Control 16, 20, and 24 were collected following the same steps.

The additional replicates of the lines collected after Generation 21 (all replicates of all Lines collected were called an Assay replicate) would run alongside Generation 22. The Assay time duration for testing is set at a strict 1.5 hours, but start and stop time were recorded for accuracy. As the eggs to populate the next generations were not taken from the Assay replicates, the time limits were short for the sake of sanity in counting the replicates.

The A- Line Assay replicates would get 3 replicate cages of the 2G and 2A slides, 3 cages of one hue disk of each Violet (V), one B, one A, one G, and One Yellow (Y) hue

disk on a slide (Outlined in Figure 6), and 3 replicate cages of 2B, 2A, and 2G on a slide. The five choice Assay is depicted in Figure 12, where any combination was randomly assigned to any Assay, not all seen in Figure 12.

The B- Line Assay replicates get 3 cages of 2B, and 2A slides, 3 cages of one hue disk of Violet (V), one B, one A, one G, and One Yellow (Y) hue disk on a slide, and 3 cages of 2B, 2A, and 2G on a slide.

The C- Line Assay replicates get 3 cages of 2G, and 2A slides, 3 cages of 2G, and 2A slides, 3 cages of one hue disk of Violet (V), one B, one A, one G, and One Yellow (Y) hue disk on a slide, and 3 cages of 2B, 2A, and 2G on a slide.

Both the Color Control Line and the Food Control line Assay replicates get 3 cages of 2G, and 2A slides, 3 cages of 2G, and 2A slides, 3 cages of one hue disk of Violet (V), one B, one A, one G, and One Yellow (Y) hue disk on a slide, and 3 cages of 2B, 2A, and 2G on a slide.

After every generation, the photographs were labeled and stored in properly labeled file designations, and copied onto two other external hard drives. The primary photos were stored on the Lab external hard drive that remains in the lab. The first copied external drive is stored off sight and never removed. The third external drive is used as a go between of drives to transfer photos to the secondary external drive. The third drive is portable, and is used to count the eggs on each plate whenever time can be allot to count them. All egg counts were recorded on distinct separate data sheets. These sheets group plates by line and generation, both hue disk and location were recorded on the data sheet, but location of the plate on the photograph does not indicate the location of the plate in the cage. An example is shown in Appendix 3. Each generation of each line will be

assessed on preference of hue, determined by the equation: [(Total Eggs Laid on Hue A)/Total Eggs Laid] = Preference A. Each generation of each line will also be assessed on locational preference. Additionally as time is recorded, egg laying rate will be calculated as number of eggs laid per minute.

2.2. Selection experiment.

The treatment that was selecting for the Aqua hue, when given a choice between Aqua and Blue hues, were designated as "A Lines". These lines were attempting to select for preferences in color in the higher wavelength-hue graph. It was predicted that after 22 generations, the preference for Green would be higher than Blue or Aqua in a three choice novel designation, Green would be preferred over Aqua in a novel two choice designation, and if a novel environment of five choices were offered with the hues of Violet, Blue, Aqua, Green, and Yellow then it was predicted that the flies would prefer yellow over green, but some eggs would be laid in an ascending scale up the hue-wavelength chart. See Figure 13 for the predicted preferences of the A Lines.

The treatment that was selecting for the Aqua hue, when given a choice between Aqua and Green hues, were designated as "B Lines". The selective pressure treatment for these lines was to produce a preference for lower hue-wavelengths. It was predicted that these lines, after the 22 generations, would prefer a novel Blue hue over the Aqua hue in a two choice model, and prefer Blue over Aqua and Green in a three-choice novel environment. Additionally, if the five choice novel environment was introduced (as described above), then the preferences should increase as the wavelength-hue decreases. These predictive behaviors are shown in Figure 14.

The last designation for selective treatments, were named the “C Lines” and these lines were selecting for Aqua preference, when the environment offered a choice between Blue, Aqua, and Green hues. The selective pressure was predicted to produce preferences for ‘middle’ wavelength-hues in the experiment. When the lines had undergone 22 generations of selective pressure, then the lines would be introduced to novel two choice selection, one with Blue and Aqua Hues, and the other with Aqua and Green hues, and a novel five hue color choice environment. In all three of these assay tests, the C Lines were hypothesized to prefer the middle wavelength hue over all other options. These predicted behaviors are depicted in Figure 15.

The first of the two control designations was a “Color Control”. These Color Controls would be given the same three choice environment as the C Lines, however no selective pressure would be induced on these lines. Instead an equal number of eggs from all hues were used to perpetuate each of the generations. The Color Controls were predicted to not prefer any one hue, and should prefer all hues equally after 22 generations, which is shown in Figure 16. So when novel hues would be introduced to the Color Control lines in the assay experiments, they would be preferred in an equal way to all the standard hue colors.

The second set of controls were completely isolated from the Experimental Evolution trials. These lines would not see any hue disk or agar plate, and were given only the standard fly food plates during the same time that the other treatments received their hues and agar plates, though they were knocked into the same type of cage, and were given food under the Hitlights LEDs with the other controls and treatment groups for the same amount of time. Designated as “Food Controls” they were a backup of

controls that were assumed to retain the wild type preferences for the hues, which would be documented and seen during the Assay trials. The Food Controls were a secondary backup for the Color Controls, as it may have been possible for the Color Controls to develop a preference by just being introduced to hue colors, or undergo a genetic drift due to equal selective pressures. These Food Control lines were still perpetuated by eggs laid during the same time as the other lines, and the lines were living in the same cage type as the other lines. This was an attempt to reduce the total differences within all the lines to only the changes in food/hue.

2.3. Assay test methods.

After selection/generation 21 trials, a new Fly Food petri dish with 50 mL of Fly Food were given to the A- Lines, B-Lines, C-Lines, and Control Lines 1, 5, and 9, and Control Lines 13, 17, and 21. The lines were left alone for 12 hours to lay eggs on the new food. After the 12 hours nine additional replicates of the A-Lines and B-Lines were collected, and twelve additional replicates of the C- Lines and Controls. After selection/generation 22 runs normally (alongside the replicates collected after generation). After generation 23 numerical lines 3, 7, and 11, as well as Control 15, 19, and 23 were collected following additional fly food being in cages for 12 hours. After generation 24 numerical lines 4, 8, and 12, as well as Control 16, 20, and 24 were collected following additional fly food being in cages for 12 hours. Any additionally collected lines were labeled as assay lines.

Assay lines were run for 1.5 hours, and the time started and finish were recorded on data sheets.

2.3.1. Data processing.

After every generation, the photographs were labeled and stored in properly labeled file designations, and copied onto two other external hard drives, the primary photos were stored on the Lab external hard drive that remains in the lab. The first copied external drive is stored off sight and never removed. The third external drive is used as a go between of drives to transfer photos to the secondary external drive. The third drive is portable, and is used to count the eggs on each plate whenever time can be allot to count them.

All egg counts were recorded on distinct separate data sheets. These sheets group plates by line and generation, both hue disk and location were recorded on the data sheet, but location of the plate on the photograph does not indicate the location of the plate in the cage or the hue disk it was paired with during the selection (Appendix 3).

Each generation of each line will be assessed on preference of hue, determined by the equation: [(Total Eggs Laid on Hue A)/Total Eggs Laid] = Preference A. Each generation of each line will also be assessed on locational preference.

3.0 Results

3.1 Experimental evolution selections.

For each of the treatments, and their replicates, a series of selection graphs were maintained. The graphs were designed to determine the replicate's individual preference over the generations for the Aqua hue. This was calculated by individual generation, and

was calculated by the equation: (Total number of eggs laid on Aqua Hue)/ (Total Number of eggs laid on all hues) = Preference for Aqua Hue. The y-axis represents the preferences for Aqua. And the x-axis is the generations of the experimental evolution treatments, and then connected by a line to each calculated preference.

For the A Lines, a graph showing the preference for aqua every five generations is shown in Figure 17A. This graph also includes the Null hypothesis line to indicate that in a two choice paradigm, that a preference for a choice without an inherent bias/innate preference should be equal to 0.5, or that there is a 50% random chance that the eggs will be on Aqua without any other factors affecting the choice. This figure combines all of the A Line replicate into a single graph. To see all of the individual replicates per generation, see Appendix 4. The A Lines were analyzed with the replicate line as a random effect, and the individual generations (all of them) as a factor, shown in Table 2. Figure 17C is the graphical representation of the Aqua preference for the A Lines for every generation.

For the B Lines, a graph representing the preference of Aqua every five generation is shown in Figure 17B. Included is a dashed Null hypothesis line, which was determined the same way as the Null hypothesis line for the A Lines. Figure 17B combines all of the B Line replicates into a single graph, but the separate replicates per all generations can be seen in Appendix 3. The B Lines were analyzed using the same rules as the A Lines and this can be seen in Table 3. Figure 17D is the graphical representation of the Aqua preference for the B Lines for every generation.

The C Lines could not be calculated the same way as the A or the B Lines, as the Null hypothesis of the C Lines (because of a three-choice treatment), gave the random chance of laying eggs on the Aqua Hue at 33% (or 0.33). The graphical representation of

the C Lines preference for Aqua over the generations is seen in Figure 18A, which only shows the preferences every five generations, with all the replicates combined in a single graph. To see each individual replicate over all 25 generations please see Appendix 4. Figure 18B represents the same data as Figure 18A, except for the Color Control treatments, which individual graphs can be seen in Appendix 4. Figure 18C and Figure 18D are the C Line and Color Control Aqua preferences calculated across all the selected generations (respectively). The y-axis numbers for Figure 18 are calculated the same way as the Figure 17 axis for the Aqua Preference per generation, and the x-axis is numerated by the generation numbers.

It was determined that the Null Hypothesis graphs would not be sufficient for both the A/B Lines and the C/Color Control Lines, as the random chance (Null Hypothesis) of an egg being laid on any hue could be either 50% or 33%. So Chi squared numbers were calculated for each treatment type, and for each replicate within the treatments, and for every generation. The Observed (O) number was represented as the total number of eggs laid per generation on aqua, the Expected (E) number was determined as: (The total number of eggs laid on all hues in the generation)/(The total number of hue choices in the treatment). The total number of hue choices was 2 for the A Lines and the B Lines, and the total number of color choices was 3 for the C Lines and the Color controls, the treatment type was determined as an average of the replicates within the treatments and graphed. This can be shown in Figure 19, where the Axis was determined as each of the combined treatment types (Observed- Expected)/ (Expected) = Aqua Preference per generation, and the x-axis is labeled for each generation. This graph indicates the error bars for each generation and treatment type.

An ANOVA for the combined replicates of the treatment types was run, where the generations were also combined into a single calculated point. This is shown in Table 4, with a graph shown in Figure 19. In Figure 19, the x-axis represents the treatment type, where all the replicates were averaged into a single treatment type, and the ANOVA combined the total generations of each treatment into a single point, which represents the (Observed-Expected)/(Expected) egg numbers for number of eggs laid on Aqua, shown on the y-axis. Error bars for each treatment types are included.

While the Aqua preferences were being calculated per generation, the egg laying rates were being calculated on a per minute basis, as the total number of minutes for each trail were recorded. When this data was graphed, a pattern of increasing egg numbers was observed. So each replicate was graphed according to the number of eggs laid on each hue, and the total eggs laid per treatment over the generations. Once these numbers were graphed a linear Trendline was included for the total number of eggs laid per generation for each replicate, with the Trendline equation written in the upper right corner of each replicate graph. A sample of these graphs is shown in Figure 20, and all of the Egg Laying Rate graphs can been seen in Appendix 5. The y-axis shows the number of eggs laid per minute, and the x-axis shows the generations. As Figure 20 has only one graph per treatment type to save on space, each graph is labeled with the treatment replicate numbers.

An ANOVA for these egg laying rates was analyzed and is shown in Table 5, which indicate a significant of egg laying rates over generations ($P<0.0000001$), and a significant determination when treatments are included ($P=0.000347$). In Figure 21, the replicates of each treatment are averaged into a single line of egg laying rates over the

generations. The egg laying rates are determined as: (mean total eggs laid)/ (total minutes in trial) as this line is the combined replicates in the treatment, this is graphed on the y-axis, and the generations are labeled on the x-axis. The error bars for each generation are included in the graph.

While the preference for Aqua hues did not appear to change over the generations, no matter the treatment type, the egg laying rates of all the treatment types and the Color Controls did increase over the generations.

3.2. Post selection assays.

For the A and B Lines an additional nine repeats of each repliacte were collected over four generations, and the C Lines, Color Controls, and Food Controls gained twelve repeats of each repliacte over the same four generations. The A and B Lines were not given 12 repetes per replicate as the generational selectiion experiment was continuting during the assay experiments, and the standard two choice envioronment was continually being offered, and those egg totals were used in the assay calculations.

With the A Lines, there was the normal Aqua vs. Blue hue choice selection. Then each of the replicates were tested in three repetes for the 2-choice Aqua vs. Green hue enviornment, the three choice Blue vs. Aqua vs. Green hue environment, and a five choice environement offered two novel hues that had not been used during any slection excperiments. See Table 1 for how these hues were determined. The B Lines, had their standard selection Aqua vs. Green choice system, and the repeats of the repliactes were tested in the two choice environemnt of Blue vs. Aqua, the three choice envioronment of Blue vs. Aqua vs. Green hues, and the final five-choice environment.

The C Lines, Color Controls and Food Controls had repeats tested in both of the two choice environemnts: Blue vs Aqua, and Aqua vs. Green hues. Additional tests for the three choice environemnt Blue vs. Aqua. vs. Green hues, and the five-choice hue environmnet was tested, and the total eggs laid per hue was recorded. In Figues 22, 23 and 24, these tests were graphed by the proportional means of hue preference, where the number of repeats were averaged to each repliacte, and each of the repliactes were averaged to the Hue's preference within the treatment types being tested. The choice tests graphed the hues in each system along the y-axis.

Figure 22 shows how each treatment line, plus the two types of controls, behaved in a two choice enviroment when Blue and Aqua hues were avaiable. All but the food control lines prefered the Blue hue to the Aqua hue.

In Figure 23, another two choice assay of Aqua vs Green hues was given for testing across all of the treatment types and the two controls. All of the treatment lines and the two controls prefered the Green hue over the Aqua hue. So they like green a lot.

Figure 24 graphs the hue preferences of each of the treatment types and the two controls. In the A Lines, B Lines, C Lines, and Color Control treatment types there is a preference of Green over Blue, and both hues over Aqua. The Food Controls liked the Blue hue least, and the Green and Aqua hues about the same (with aqua maybe a tad more then green, but within the graphed error bars).

For the five-hue-choice assay tests and ANOVA was run to determine if their was a significant effect of treatment ($F_{4,55}$ =1.958, P=0.1139), color($F_{4,220}$=1.787, P=0.1324), or the interaction of treatment and color ($F_{16,220}$=1.258, P=0.2267), shown in Table 6. None of these effects showed any significance. Figure 25 graphs the mean proportional

choice of each hue by treatment type, as was graphed in Figure 22, 23 and 24 according to each of the assay choice types. The A Lines, B Lines and Color Controls in Figure 25 show no preference for any hue type over another within the error bars, but these lines could arguably prefer the Violet hue, then the Green Hue, then the Yellow hue, then the Blue hue, and they prefer the Aqua hue the least. When graphing the C Lines, they preferred the Hues Violet and Green roughly in the same proportions as the A, B and Color Control Lines, but liked Blue less than Aqua, and Aqua was preferred almost as much as the Violet hue, and more than the Green hue. However, with the C Lines the Yellow hue was preferred more than any other hue, and that was unique to the C Lines alone. The Food Controls preferred the Green hue the most, followed by Aqua, Violet, Blue and Yellow hues in order. Though the individual mean proportions of the Hue preferences can indicate a unique variation in the C Lines and the Food Controls, both fall within their combined error bars of the other treatment types.

In summary of the assay charts, when a treatment type is graphed and the Green Hue is available, they will choose the Green hue in spite of all other choices. The Food Controls are the only treatment that do not follow the other treatment preference lines. So the introduction of color choice hues (even if the hues are not being used to induce selective pressure), in an experimental evolution study does cause some type of behavioral change.

3.3. Data summary.

No change in preference was seen across evolutionary time during the selections.

None of the expected/predicted preferences were shown in the Post-Selection Assays. For instance, flies evolving in a situation where aqua is better than green don't show an enhanced preference for blue, and not even for the selected aqua over green.

All of the lines with treatments that included color choices evolved a stronger preference for green in comparission to Baseline Data (Appendix 1) and Food Controls.

Egg laying rates increased over evolutionary time, and the greatest increases occurred when more color choices were available, in comparision to Food Controls.

4.0. Discussion

4.1. Choosing all the options & bet hedging.

Color preference doesn't appear to have responded to selection in the way in that was predicted. In the assays, aqua should have been preferred over at least one other hue disk, and it wasn't. Everyone seems to like green when that choice is offered in the assays. And even going back to look at the selection data, we also don't see a change across generations as predicted (that aqua becomes more preferred as the generations continue). All of the flies in the selection treatments did appear to have solved the problem of preferential hue selection with a non-behavioral solution: they have increased fecundity across evolutionary time. In other words they laid more eggs each generation across all the choices presented to them. This egg laying rate increase is affected by the treatment, as there is a steady increase in the total number of eggs laid by each line across all generations (including the Color Controls).

4.1.1. Why green?

When the preliminary testing was done to determine if the flies could undergo Discrimination Conditioning based on hue colors, where quinine was used as an adverse/punishment phase in one hue of a two choice hue system, which was unsuccessful. In addition to the conditioning experiments a set of 'control" lines were given a two choice test with two of six hues, which amounts to six different preference tests; Blue vs. Aqua, Aqua vs. Green, Blue vs. Green; and two other hue disks were used that were supposed to be closer to the Aqua hue by their wavelength determination, so a (Blue-Aqua) vs. Aqua, Aqua vs. (Aqua-Green), and (Blue-Aqua) vs. (Aqua-Green), which showed no major preferences towards any one hue in any of the preference testing combinations. The general preferences skewed so that at least one hue was preferred 55% of the time.

However, we do know that they like green. Green is the predominate color of the natural ecosystem that fruit flies evolved in. Green is a very common color in a non-Laboratory setting, and it is possible that when the flies are presented with a novel choice paradigm, that their instinct is to go to green.

4.2. Fecundity & egg laying rates.

Fecundity is a combination of both the fertility of a species and the fitness of the species, as fecundity can be controlled by the genes and the environment. In the case of *Drosophila melanogaster* the fecundity is determined by the total number of eggs a female lays in her lifetime, and the environment that those eggs are laid in.

In the case of a variable environment, the production of more offspring increases the chances of some of the offspring making it to adulthood, and even more so if the

number of male partners has increased. This trade of for specialized offspring with specific benefits is reduced to attempt to increase the fitness of offspring in multiple environments or environments of high selective pressure and variance (Deng, et al., 2012; Fox & Rauter, 2003). Foucaud, et al. (2016) conducted an experiment to specifically calculate fecundity and learning during an invasion by a novel *Drosophila sububscura* population to a native *Drosophila sububscura* population. While both species preformed roughly the same in cognitive learning abilities, the invasive species had a higher fecundity than the native population.

4.3. Why didn't color preference evolve?

While it was shown that color preference did not evolve in any of my treatment lines, why this happened is unknown at this time. It is possible that the wild type population didn't have the initial genetic variability to allow for color vision preference and evolution of preference in these fly lines.

It is possible that too few generations were under selective pressure for behavioral preferences to evolve. While the genetic variation could have change a little it would not have been enough to show in significance if there were not enough generations (or time) for the behavioral phenotype to be expressed. In Dr. Dunlap's lab, when Learning Tests are being performed, the fly lies are not analyzed for behavioral changes until they have undergone at least forty generations of selective pressure.

However, there is the Russian domesticated fox (fox farm) experiment, where fur farm foxes (*Vulpes vulpes*) underwent strong selective pressure for tameness. In this case only the foxes that were the tamest of the lot were allowed to breed, and in the first

generation there was nearly all aggressively fearful or avoidant of human contact, but it is noted that by the third generation the aggressiveness had been eliminated from the breeding population. While this experiment is more complex than described, this is a strong selective pressure on a behavior, and by the sixth generation some foxes had developed an attractiveness to human contact, seeking it out, and developing behaviors that gained it attention from the researchers. These behavioral elite foxes also developed morphological changes in ear floppiness and fur color patterns (to become cuter to the experimenters), and their sexual behaviors changed, they matured a month faster they had a longer breeding season, and on average produced one more pup per litter than the standard fur farm fox (Jones, 2016). So if these experimenters could see morphological, sexual, and behavioral changes under strong selective pressure in less than 10 generations, why did my experiment not produce noticeable behavioral preference changes at any point in the experiment? Additionally in Mery & Kaweki's (2002) paper, they were able to observe evolution in learning ability in *Drosophila* within eight generation.

Though a behavior was altered during my experiment; egg laying rate. As the Experimental Evolution study progressed on generational time, all of the treatment lines and the color control lines showed a significant increase in the number of eggs laid within each line. So, each of the lines behaviorally produced more eggs in the same timespan than their earlier generational ancestors. It is possible that fecundity responded to the selection pressure because it may be the first behavioral trait that could be affected by selective pressures. Or the genes that are responsible for fecundity naturally have more variability and are more responsive to changes in selective pressure in an environment, or

the genes are the most plastic of the *Drosophila melanogaster* traits, so it is more likely to alter phenotype because of selection pressures. And if fecundity is the first behavioral trait to be affected by selection pressures, it is possible that if fecundity is being altered by the treatments (is responding), then color preference response could be lessened. This could mean that if one behavior is taking on the full force of the selective pressure, the other behaviors may not alter as readily because the one behavior is responding, even if it is not the behavior we hoped to select on.

There is also the possibility that the genes involved in color vision and color preference behavior are pleiotropic, or participate in other behaviors or phenotypic traits. These other traits could be highly conserved and even show redundancy to prevent variations. Additionally, the genes for color vision could be downstream of other activation genes that cannot be altered as readily as fecundity. In Chapter 1 I discussed the many genes of eye morphology (Arendt & Wittbrodt, 2001; Arendt, 2003; Bao & Friedrich, 2009; Bazin-Lopez, et al., 2015; Blanco, et al., 2009; Fernald, 2006; Gehring & Ikeo, 1999; Hoshiyama, Iwabe & Miyata, 2007; Kozmik, et al., 2003; Rister, Desplan, & Vasiliauskas, 2013; Treisman & Herberlein, 1998; Weasner, et al., 2009; Yang, et al., 2009a; Yang, et al., 2009b), and the major gene controlling this is the *Pax6* gene, which is found in most animals and insects for controlling eye development, with not much variations. Additionally, some of the other genes which segment and activate the structures of the eye, will sometimes be involved with the development of the heads, brains, antennae, ears and nose of their corresponding species. So some genes contribute to the development of two or more sensory systems, and that pleiotropy could prevent

selection on any of the color genes, if they would alter the formation of another sensory system as well.

Issues with available nutrients could prevent any preferences from developing at all. In the case of *Drosophila* vision if vitamin A is lacking in the media the eggs/larva are reared on then vision could not develop because opsins are vitamin A derivatives. So it is possible that in tandem with genes that cannot develop specific components of vision, those genes could not have the proper materials to work with. This could also prevent some genes that are shown to be working properly through sequencing, to not function at all.

There are other genetic restrictions that could have prevented selection. As explained in Chapter 1 (Dulia, et al., 1999; Frentiu, et al., 2007b; Zhang, 2003), the reason for another species to gain another level of complexity of color vision- dichromats to trichromats- is due to a duplication even of one of the genes of opsin, and then the specialization of the duplicated gene to another maximum wavelength of light. So before the specialization could occur, or evolution of preference, there must first be that duplication event. That initial redundancy of opsin genes allows for the threshold of signal detection theory to be altered to prevent misses while retaining the original threshold criteria on the original gene.

4.4. Other possible explanations.

In regards to the increase of Egg Laying Rate over time, there are a few minor possibilities for what could have caused this.

The first explanation is the possibility that more eggs were moved every generation, getting exactly 80 eggs per vial could be difficult and it is reasonable that a few extras could have been added. However as the strict 80 eggs per vial (480 eggs per Line) was maintained throughout the Experimental Evolution study, any excess eggs would be less than 10 eggs per vial every generation and would not account for the drastic increase in the egg laying rate over the generations.

It is possible that the ratio of females to males in the Lines was increasing over time. In other words the number of females was increasing over time and the number of males were decreasing over time. This is possible to account for the number of eggs laid per line/ per Treatment type, but I am unable to verify this as I did not determine what the female to male ratios were each generation.

4.5. Summary.

Color vision may be very difficult to change. It could be that color vision itself cannot evolve because there is not a selective pressure strong enough to influence it without some additional genetic duplication event first. It is also possible that the plastic responses to the changes in the environment are more readily apparent in fecundity and not in behavior first. So it is possible that by continuing this strong selection pressure on color vision preference to 40 or more generations could have indicated a change in that color vision preference that the 22 generations of my research did not.

Additionally, the selective behavior in a two- or three- choice paradigm may not be the best conditions of evolution of color vision, so another behavior task that involves color vision and selective pressure could have produced a more noticeable change in the

behavior than my experiment resulted in. It is also possible that fecundity is the only behavioral result that selective pressure on color vision would produce, only because the genes that are involved with the development of color vision are directly involved in the construction and development of other senses.

Fecundity research should be investigated more thoroughly, as it appears that in the Russian Fox Experiment that sexual behavior evolved with the tameness under their strong selective pressures. As sexual behavior was shown in my experiment as one of the only significant changes over time, sexual behavior and fecundity may have shown that evolution has occurred.

Any of these reasons would be cause for further study of strong selection experiments on color vision preferences to determine the actual behavioral changes that develop and are key to determining evolution.

Tables

Table 1: Wavelength to RGB-Hue Conversions Used for Disk Colors

Wavelength (λ)	RGB Hexadecimal			Single Letter Designations Used In The Experiments (And The Color Reference)
	R	G	B	
405 nm	130	0	200	V (Violet)
440 nm	0	0	255	B (Blue)
475 nm	0	192	255	A (Aqua)
510 nm	0	255	0	G (green)
562.5 nm	201	255	0	Y (Yellow)

Table 2:

Effect	Univariate Tests of Significance for P(Aqua) (A lines in Mellissa Selection Data.stw) Over-parameterized model Type III decomposition **Effect (F/R)**	SS	Degr. of Freedom	MS	Den.Syn. Error df	Den.Syn. Error MS	F	p
Intercept	Fixed	15.03395	1	15.03395	11.0000	0.022708	662.0577	0.000000
Line	Random	0.24979	11	0.02271	276.0000	0.038184	0.5947	0.832754
Generation	Fixed	0.06166	1	0.06166	11.0000	0.015600	3.9526	0.072258
Line*Generation	Random	0.17160	11	0.01560	276.0000	0.038184	0.4085	0.951779
Error		10.53887	276	0.03818				

Table 3:

Effect	Univariate Tests of Significance for P(Aqua) (B lines in Mellissa Selection Data.stw) Over-parameterized model Type III decomposition **Effect (F/R)**	SS	Degr. of Freedom	MS	Den.Syn. Error df	Den.Syn. Error MS	F	p
Intercept	Fixed	10.06760	1	10.06760	11.0000	0.021402	470.3969	0.000000
Line	Random	0.23543	11	0.02140	276.0000	0.035594	0.6013	0.827286
Generation	Fixed	0.00525	1	0.00525	11.0000	0.015085	0.3482	0.567069
Line*Generation	Random	0.16593	11	0.01508	276.0000	0.035594	0.4238	0.944917
Error		9.82408	276	0.03559				

Table 4: ANOVA of ((O-E)/(E)) for Each Treatment Group Over the Generations

Effect	Repeated Measures Analysis of Variance ((O-E)/E in Sigma-restricted parameterization Effective hypothesis decomposition				
	SS	Degr. of Freedom	MS	F	p
Intercept	64.8363	1	64.83632	613.4718	0.000000
Treatment	4.3546	3	1.45152	13.7341	0.000002
Error	4.6503	44	0.10569		
GENERATI	3.4422	24	0.14343	1.1550	0.275288
GENERATI*Treatment	9.5697	72	0.13291	1.0703	0.327070
Error	131.1372	1056	0.12418		

Table 5: ANOVA for Egg Laying Rates

Effect	Repeated Measures Analysis of Variance (Egg Laying Sigma-restricted parameterization Effective hypothesis decomposition				
	SS	Degr. of Freedom	MS	F	p
Intercept	515182.0	1	515182.0	675.0554	0.000000
Treatment	20464.6	3	6821.5	8.9384	0.000097
Error	33579.5	44	763.2		
GENERATI	89462.6	24	3727.6	28.8093	0.000000
GENERATI*Treatment	15868.3	72	220.4	1.7033	0.000347
Error	136635.0	1056	129.4		

Table 6:

Effect	Repeated Measures Analysis of Variance (Spreadsh Sigma-restricted parameterization Effective hypothesis decomposition				
	SS	Degr. of Freedom	MS	F	p
Intercept	12.51562	1	12.51562	4517.768	0.000000
treatment	0.02169	4	0.00542	1.958	0.113886
Error	0.15237	55	0.00277		
COLOR	0.07020	4	0.01755	1.787	0.132351
COLOR*treatment	0.19755	16	0.01235	1.258	0.226703
Error	2.15998	220	0.00982		

Figures

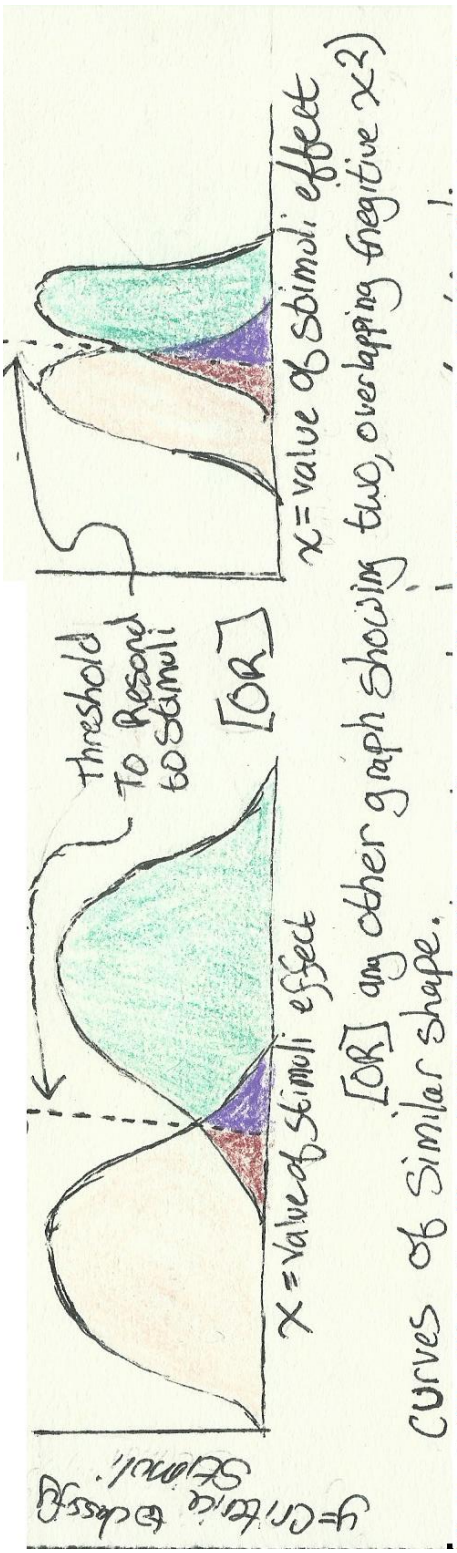
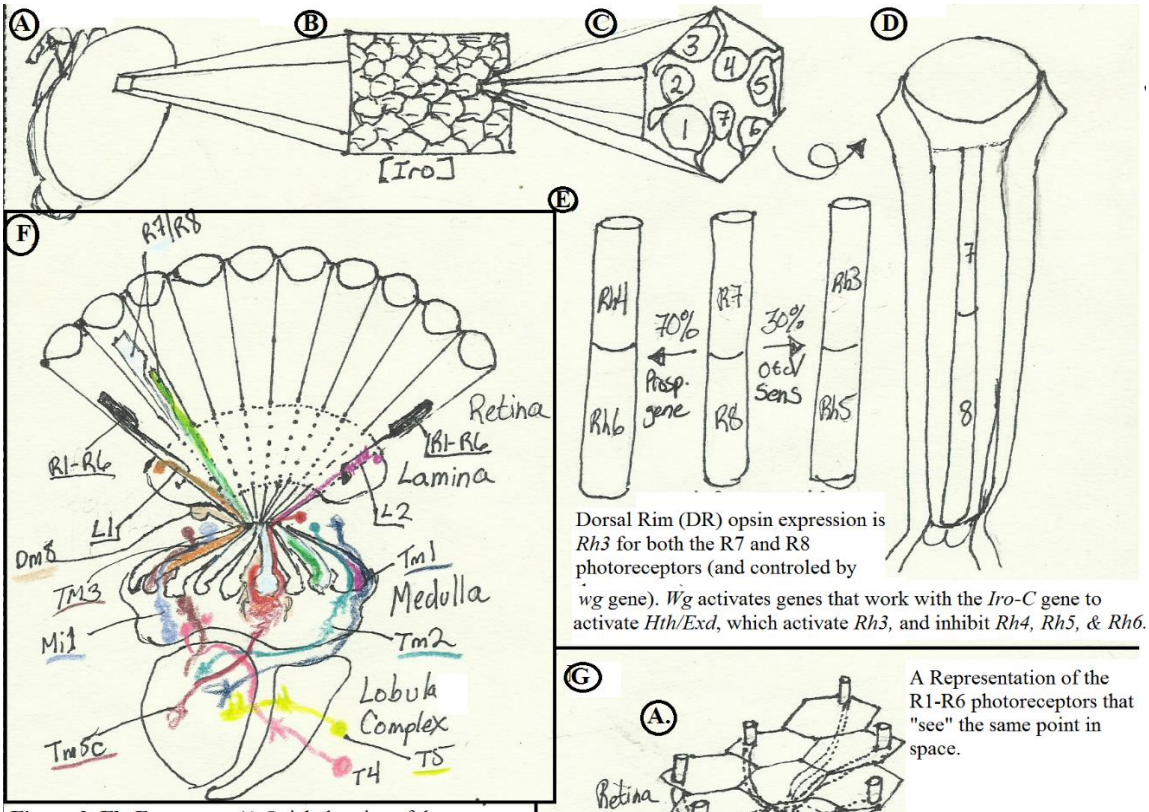
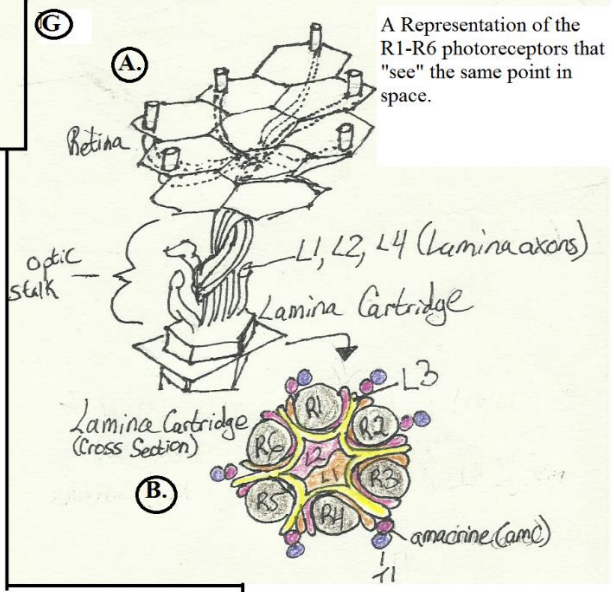


Figure 1: Signal Detection Theory (SDT) IN the SDT graphs above, the yellow shadded cuve of the stimuli can be categorized as noise; the green curve represents a signal; the overlapped red-shadded ara represents signals that are missed because the individual considered it noise; on the other side, the violet-shadded overlapped area, is noise that is regarded as a signal that the individual responded to or "false alarms". The Threshold line is specific to each individual or species, and is "calibrated" for the number of missed signals the individual/species is "willing" to accept in combination with the highest number of false alarms it will respond to. If that threshold line were to move to the right of the graph, to never miss a signal, there would eb an increase in the area of false alarms- or more energy/time expended for noise to garenttee no missed signals.
Consulted references for this image: Abdi, 2007; Bowmaker, 2008; Endler & Basolo, 1998; Garland & Kelly, 2006; Goldsmith, 2013; Shettleworth, 2010.



Dorsal Rim (DR) opsin expression is *Rh3* for both the R7 and R8 photoreceptors (and controled by *wg* gene). *Wg* activates genes that work with the *Iro-C* gene to activate *Hth/Exd*, which activate *Rh3,* and inhibit *Rh4, Rh5, & Rh6.*

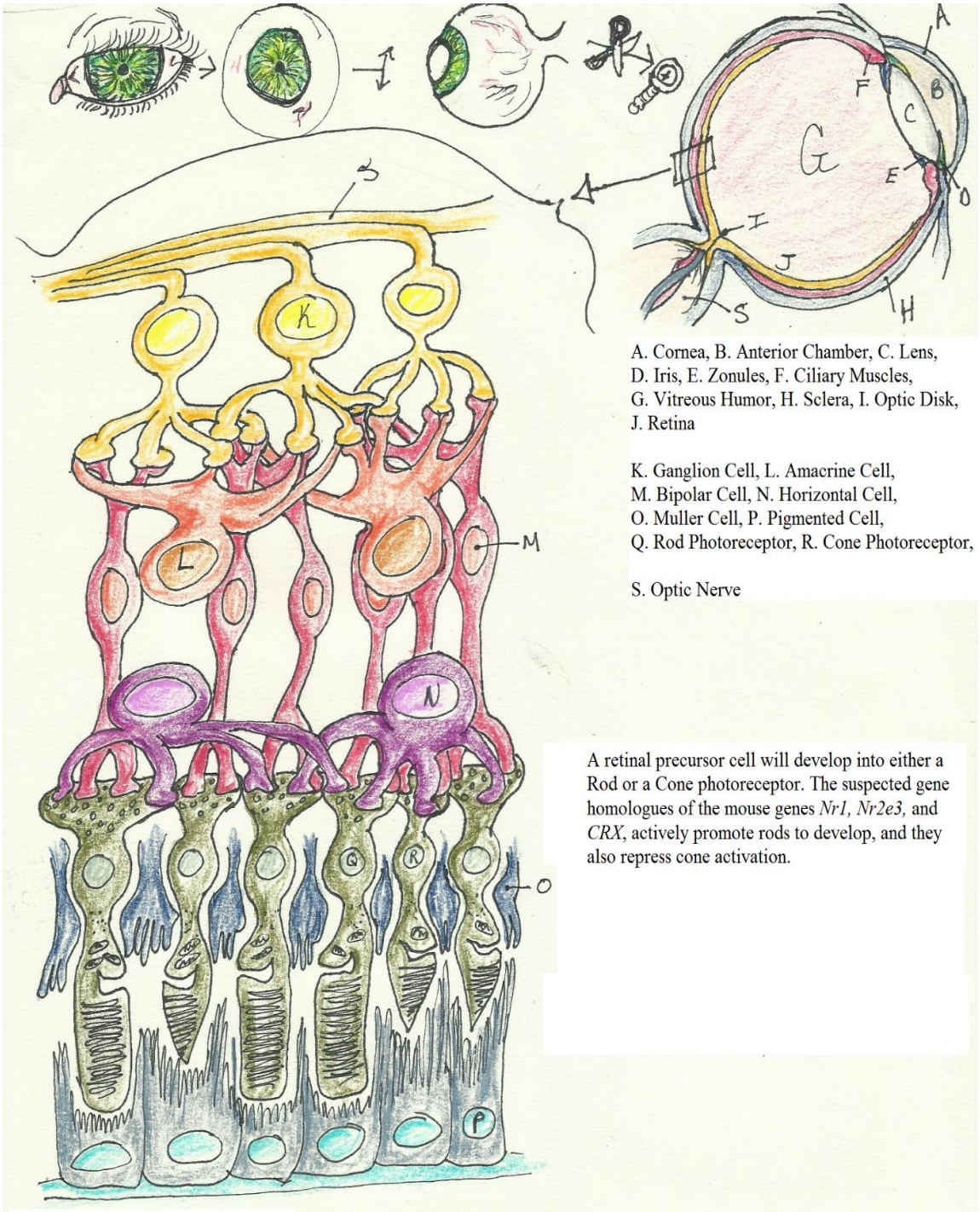


A Representation of the R1-R6 photoreceptors that "see" the same point in space.

Figure 2: Fly Eye. **A)** Quick drawing of the *Drosophila* head. **B)** A representation of the fly eye under a microscope, where the Ommatidia facets are easily shown as segments, and where the gene family *Iro* controls ommatidia location on the eye field. **C)** A top view of an ommatidium showing the eight photoreceptor locations, where R7 is on top of R8. **D)** The side view of a general ommatidium, indicating how the R7 and R8 photoreceptors stack. **E)** The two major types of *Drosophila* ommaditia are determined by the opsin genes expressed in the R7/R8 complex. The R7 opsin expresion (designated randomly by the *Sal* gene) directly affects the R8 opsin expression. Approximately 70% of the ommaditium become 'yellow', where the R7 opsin expresses *Rh4*, which was activated by transcription factors, that also inhibita a singal in R8, then in R8 the stanadard gene *Warts* indirectly activates Rh6 by inhibiting other gene pathways. In the 'pale' ommatidium, the R7 genes *Otd* and *Sal* activate/enhance *Rh3*, and then a signal is sentto R8, where it activates *Melt. Melt* inhibits *Wart*, so the *Otd* and *Yki* activates the *Rh5* opsin, and *Yki* inhibits *Rh6.* In this determination the *Sal* gene activates R7 fate directly, *Sens* inhibits R7 gene activation, but activates R8, and the *Prosp* inhibits the R8 gene activations. **F)** A two-dimensional representation of the visual circuit and neural projections; R1-R6 can be synapsed with L1 axons in the Lamina, and the L1 projects to the Medulla. The L1 is synapsed with both the Tm3 and Mi1 axons. Mi1 projects to other layers of the Medulla, and Tm3 projects to the Lobula Complex, where it is crossed with the T4 axon. T4 then crosses from the Lobula to the Lobua Plate, and beyond. R1-R6 can also synapse with the L2 axon; the L2 extends from the Lamina to the Medualla, where it is synapsed with Tm1 and Tm2 axons. Tm1 and Tm2 project to the Lobula, where Tm2 interacts with T5, and T5 prjects from the Lobula to the Lobula Plate, and out of the Lobula Complex. With the R7, the photoreceptor neurons project to the Medulla, and synapse with the Tm5c and Dm8; Dm8 projects only within the layers of the Medulla, and the Tm5c projects to the Lobula. **G) A.** A diagram that shows how the R1 of one ommaditium, the R2 of a neighbor's, etc. combine their axons into an optic stalk, to represent a single point in space, that projects into the same Lamina cartridge. **B.** The Lamina cartridge cross section, to show how each of the photoreceptor neurons are oreiented and interact with the axons of Lamina neurons.

*Mast, et al., (2006), lists in their Table 1 all of the genes that regulate, maintain, and/or control the *Drosophila* visual systems.

The papers that were consulted to produce this figures were: Behnia & Desplan, 2015; Borst, 2009; Clandinin & Zipursky, 2002; Cook, et al., 2003; Desplan, 2004; Erclik, et al., 2009; Goldsmith, 2013; Hardie, 1985; Land & Fernald, 1992; Paulk, Millard, & van Swinderen, 2013; Sanes & Zipursky, 2010; Ting & Lee, 2007; Zheng, et al., 2006.



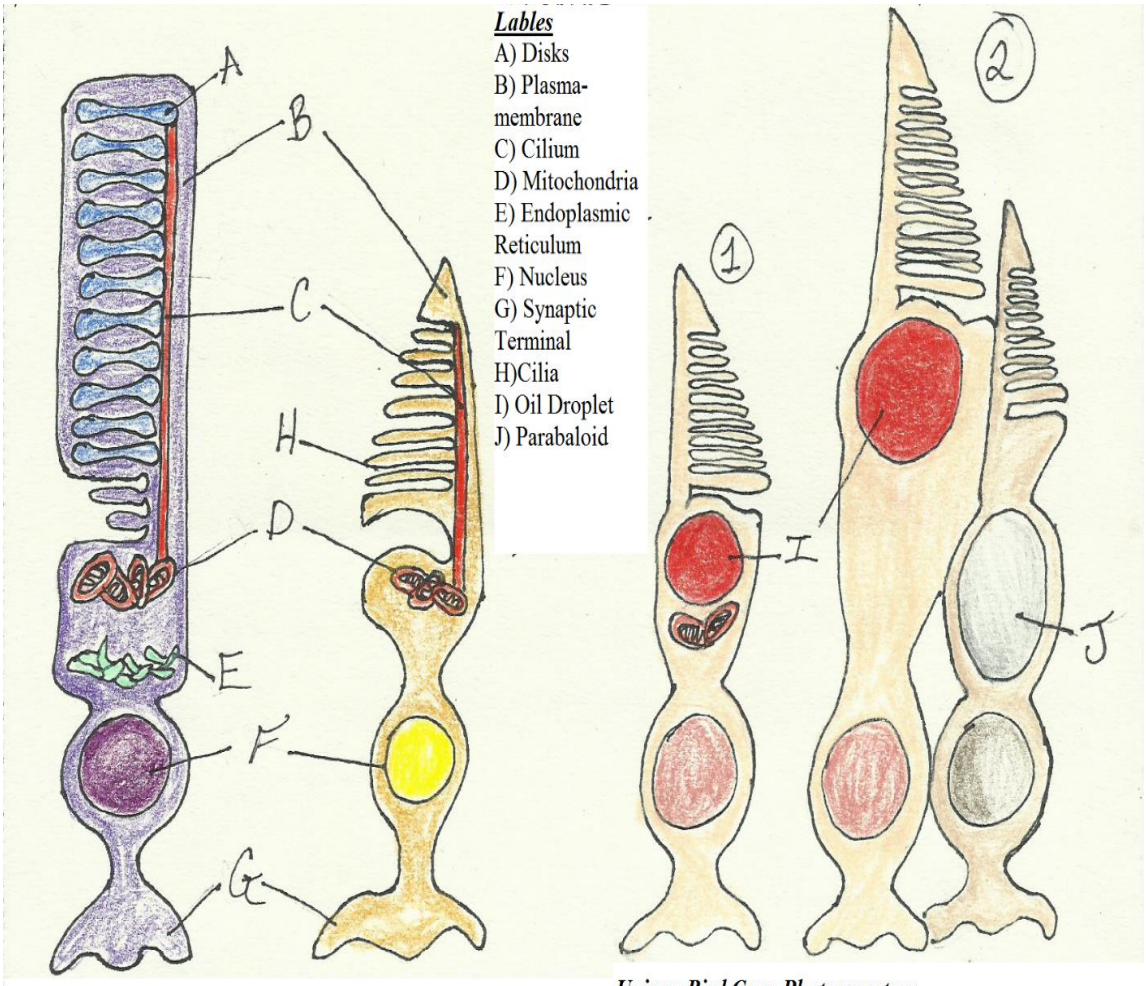
A. Cornea, B. Anterior Chamber, C. Lens,
D. Iris, E. Zonules, F. Ciliary Muscles,
G. Vitreous Humor, H. Sclera, I. Optic Disk,
J. Retina

K. Ganglion Cell, L. Amacrine Cell,
M. Bipolar Cell, N. Horizontal Cell,
O. Muller Cell, P. Pigmented Cell,
Q. Rod Photoreceptor, R. Cone Photoreceptor,

S. Optic Nerve

A retinal precursor cell will develop into either a Rod or a Cone photoreceptor. The suspected gene homologues of the mouse genes *Nr1, Nr2e3,* and *CRX*, actively promote rods to develop, and they also repress cone activation.

Figure 3: Camera-Type Eye Describes the major features of a human eye. The colors are not reflective of natural colorations found in these structures. References consulted to develop the figure: DonExodus2, 2008; Erclik, et al., 2009; Fain, Hardie, & Laughlin, 2010; Gehring, 2014; Handwritten Tutorials, 2011a; Imamoto & Shichida, 2014; khanacademymedicine, 2013b; Koyanagi & Terakita, 2014; Lamb, 2013; Lucas, 2013; Sanes & Zipursky 2010; ScienceHook, 2016; Shichida & Matsuyama, 2009.



Rod Photoreceptor
Used for Scotopic Vision (usually), with the rod responce rates being described as Large and slow, with high sensitivity

Cone Photoreceptor
Associated with color vision, and the cone's general responce rates are smaller and faster than the rod's responce rates, and the cone's sensitivites are generally lower

Unique Bird Cone Photoreceptors

1)Cones that retain oil droplets are able to filter light stimuli becasue the oil droplets are usually colored.

2) Double cones- where the principle cone contains an oil droplet and the accessory cone contains a parabaloid

Figure 4: Vertebrate Photoreceptors
Papers consulted for this image: Arendt, 2003; Fain, Hardie, & Laughlin, 2010; Goldsmith, 2013; Lamb, 2013; Shichida & Matsuyama, 2009.

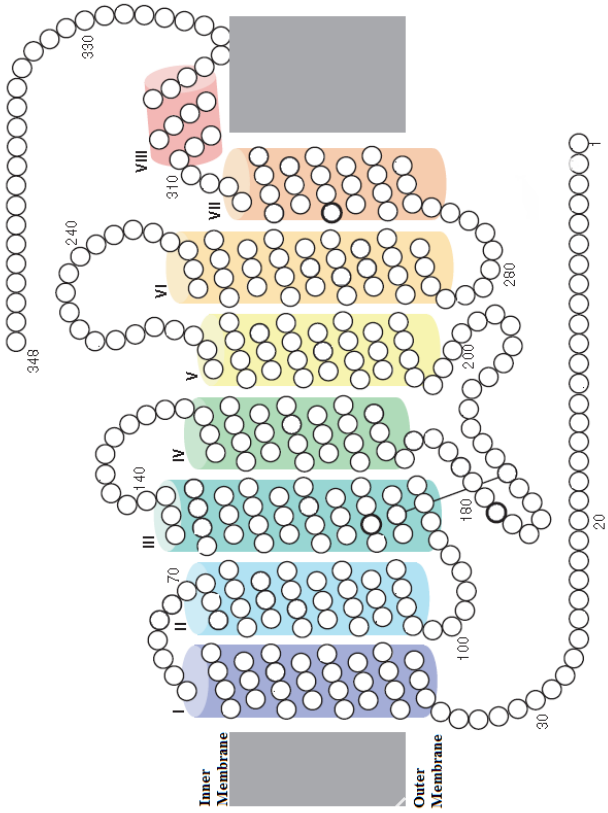


Figure 5: Opsin Amino Acid Configuration
Consulted multiple papers, and while this configuration is the bovine opsin- the first opsin Amino Acid configuration discovered. The Amino Acids were erased for a blank opsin protein.

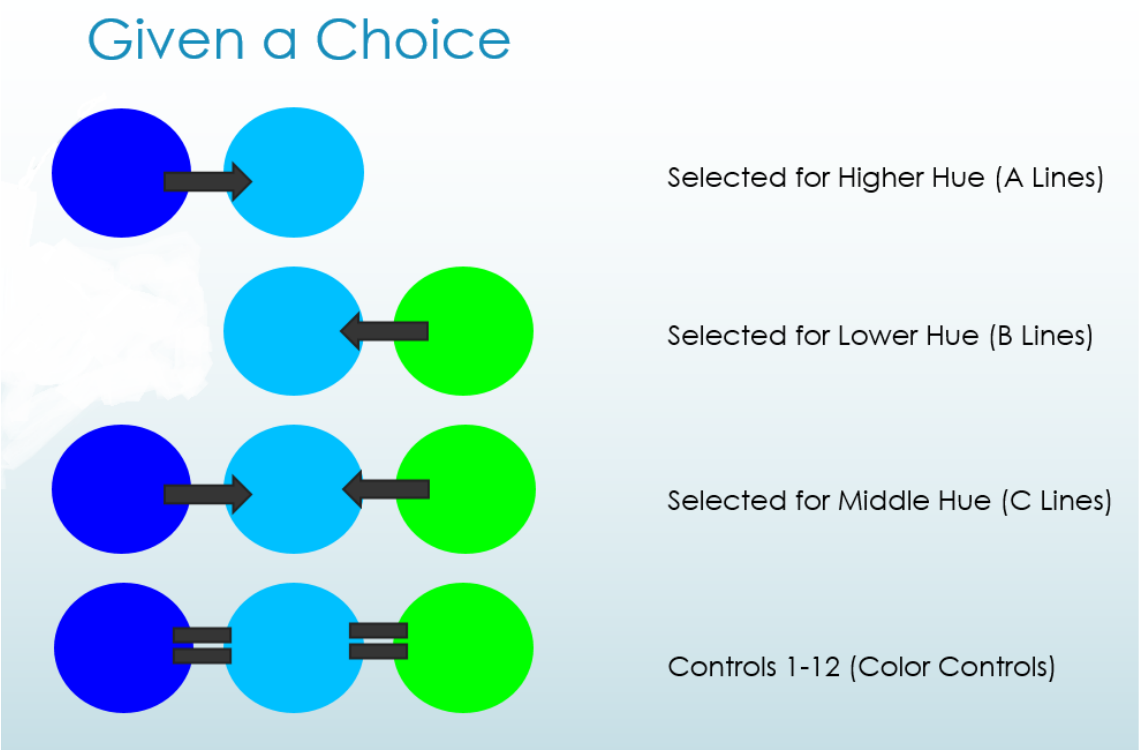


Figure 6: Treatment Types and Color Control Selections
The three treatment types are documented by the Hue Disks that were given to each Line in a Treatment and the Hue Disk that the next generation of eggs would come from. The Color Controls had equal amounts of eggs obtained from all Hue Disks.

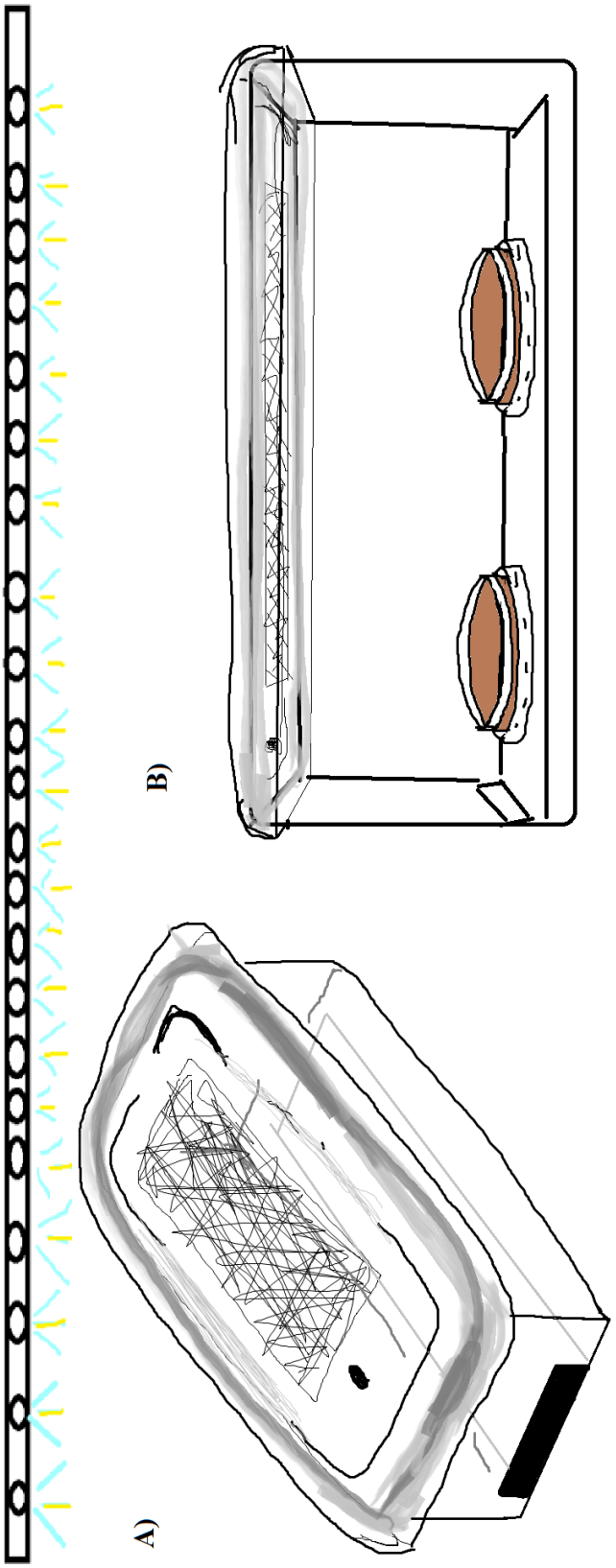


Figure 7: Fly Cages
A) A side view of a clear storage shoecase, where the lid had a hole drilled into it (Black dot), and a rectangle was removed. The square was covered by a swatch of netting, that was glued in place. The Bottom of the box had another square removed from one of its smaller walls (Black rectangle), the lid was glued to the bottom of the bod and a separate slide was placed in the box, and the hole plugged. **B)** Side view of the modified shoebox- now called a Fly Cage, with a simulated pair of fly food petri-dishes in the cage.

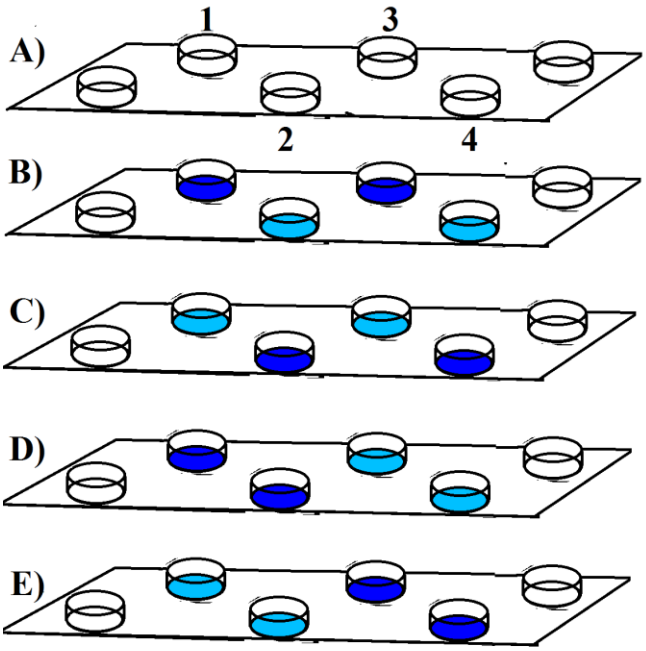


Figure 8: A Line Hue Disk Combinations
A) A Slide with Petri-dish holders glued on, and numbered for use in the A lines.
B)-E) All the possible Blue vs. Aqua choice combinations used in the A lines.

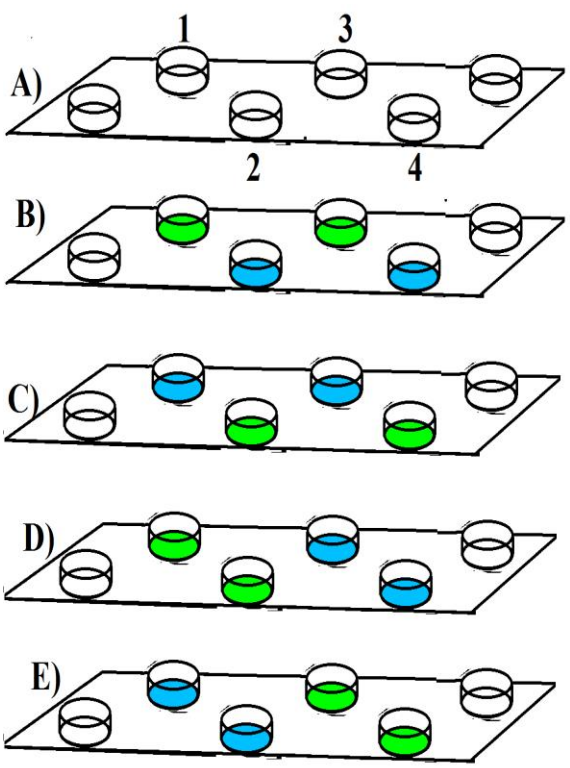


Figure 9: B Lines Hue Combinations
A) A sketched slide for hue disks and agar plates to simulate Choice selection, with the numbered holders used for B-lines.
B)-E) All of the Aqua vs Green 2 choice combinations that were used.

F) Life Photo Example of a B Line Treatment of one pattern type.

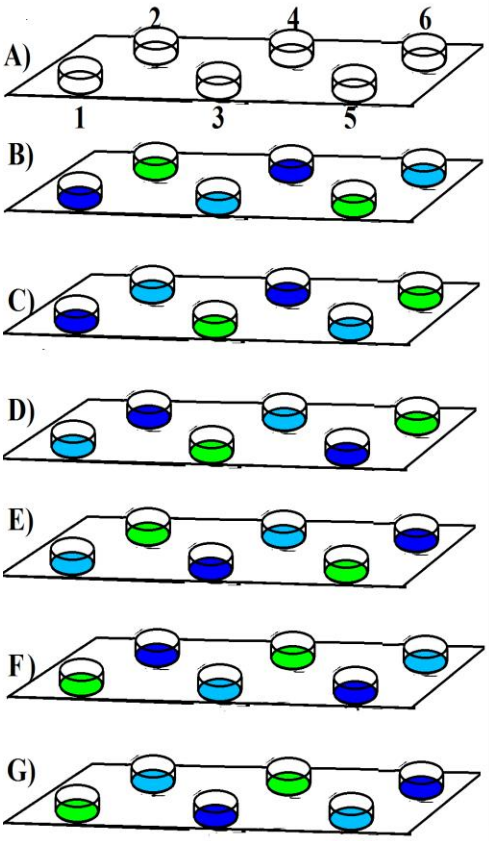


Figure 10:The C line & Color Control Hue Combinations

A) A skecthed slide, which numbers the hue+aqua holders that are used in the C line and Color Control experiments.

B)- G) All of the three hue choice combinations that were used on the C lines and Color Controls during the selections.

F) Life Photo of a 3-Hue-Choice Pattern

Both the C Lines and Color Controls were offered this type of pattern example.

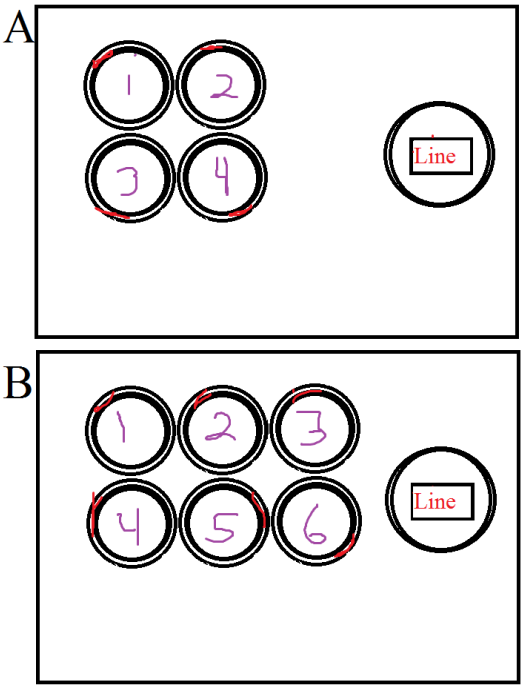


Figure11:Photographs
A diagram showing how each set of agar plates were photographed. **A)** For the A or B lines, **B)** for the C lines or Color Controls. Both photographs had a petri-dish lid with a white sticker on it, labling the line the agar plates came from in red ink. The numbers 1-4 or 1-6 did not represent the location of the plate in the cage, only how the plates were counted in the photograph.

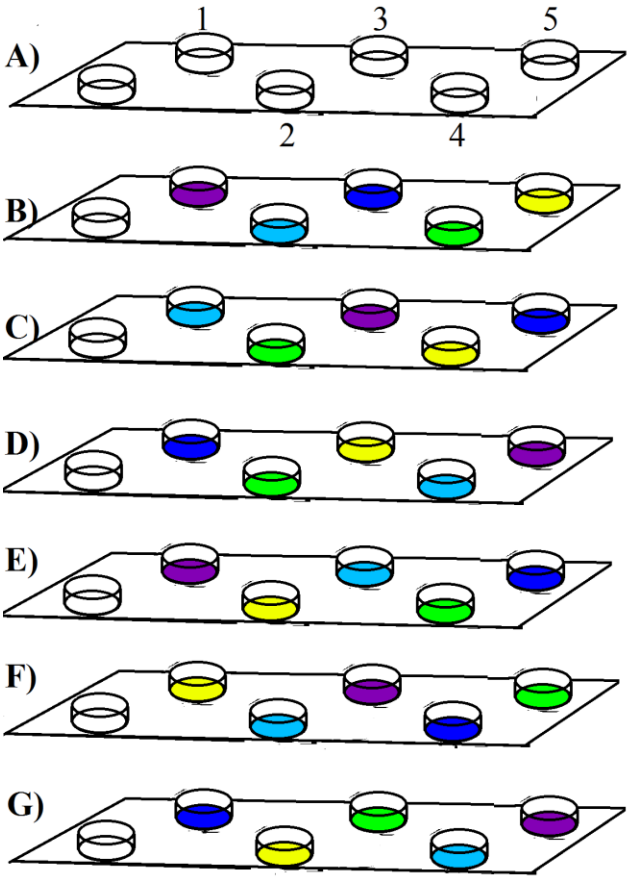


Figure 12: The Five Choice Selection
A) The numbered disk+ agar holders that were used in these five choice Assays.
B)-G) A small representation of the hundreds of orders the five hues could have taken when presented during the Assays.

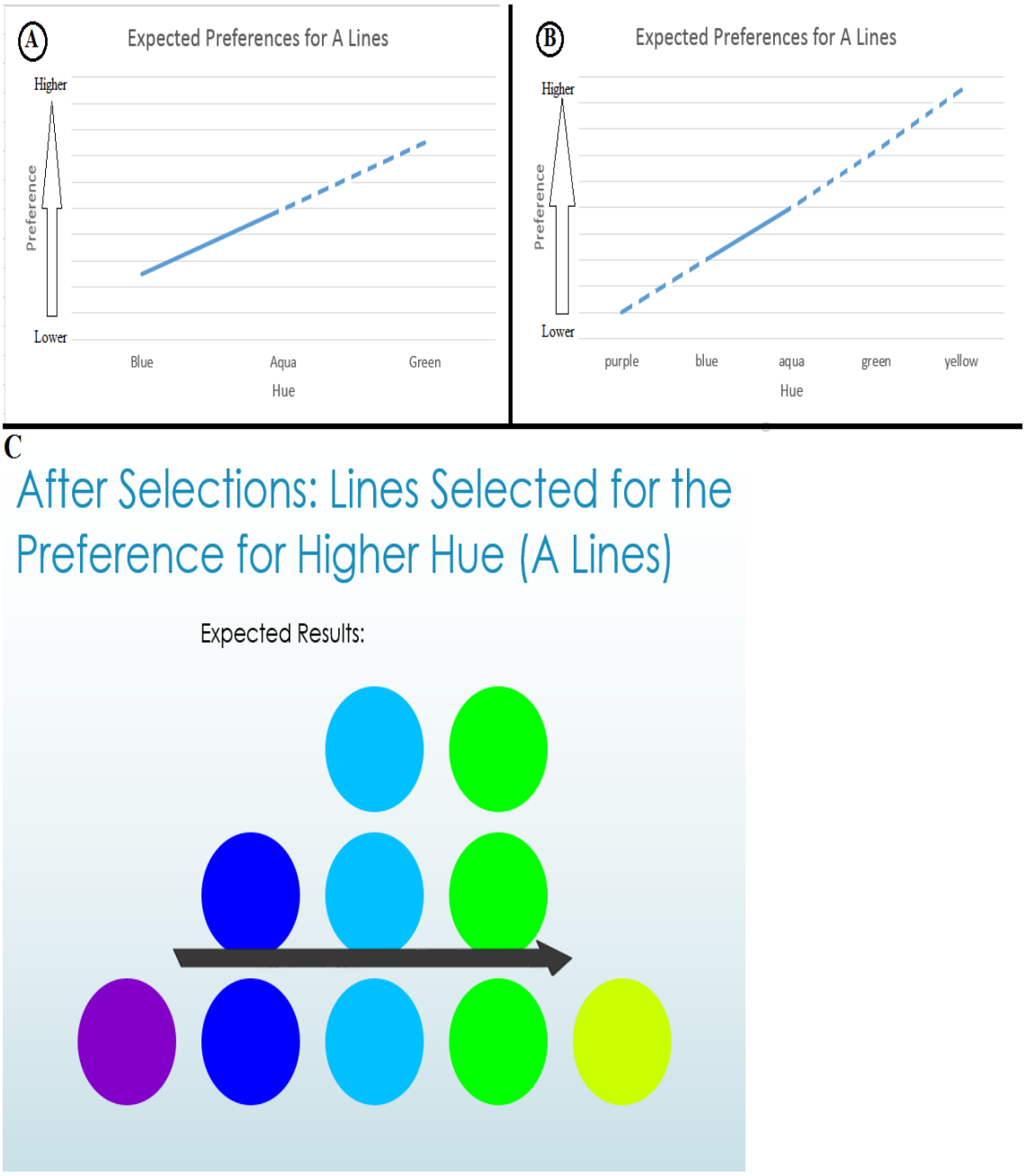


Figure 13: A Graphical Assessment of the Predicted Behavior of the A Lines After 22 Generations of Selection*; A)When the A Lines are introduced to a novel hue green, it is hypothesized that the preference of the A Lines should increase towards green, shown as the dashed line, while the A Lines normal environment of blue and aqua. B) This is a similar graph to (A), but with the five hue choices and their predicted preference values in the A lines. C) A colored representation of the preferences expected during the Assays.*

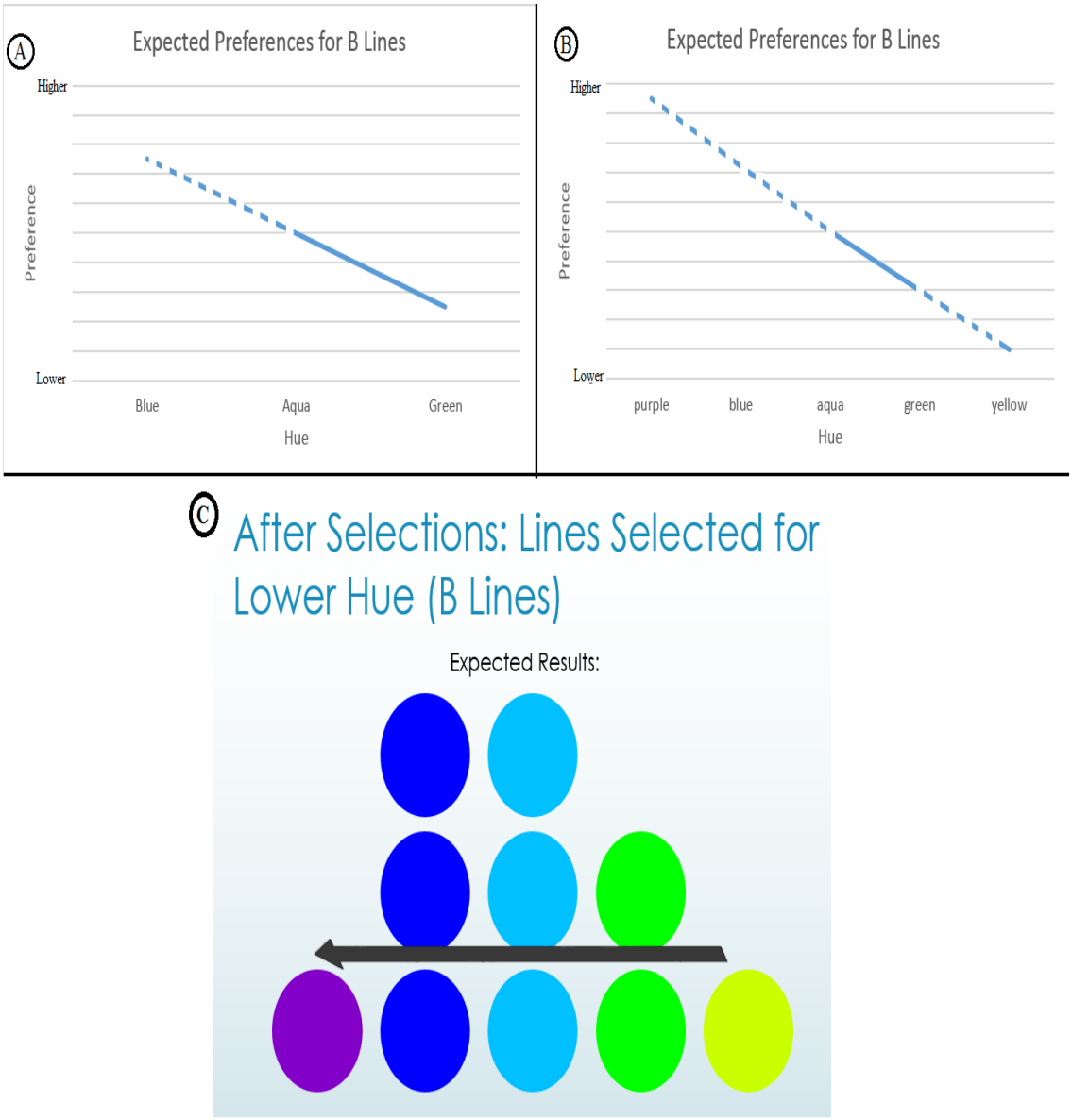


Figure 14: A Graphical Assessment of the Predicted Behavior of the B Lines After 22 Generations of Selection; *A) When the B Lines are introduced to a novel hue blue, it is hypothesized that the preference of the B Lines should increase towards blue, shown as the dashed line, while the B Lines normal environment of green and aqua. B) This is a similar graph to (A), but with the five hue choices and their predicted preference values in the B lines. C) A colored representation of the preferences expected during the Assays*

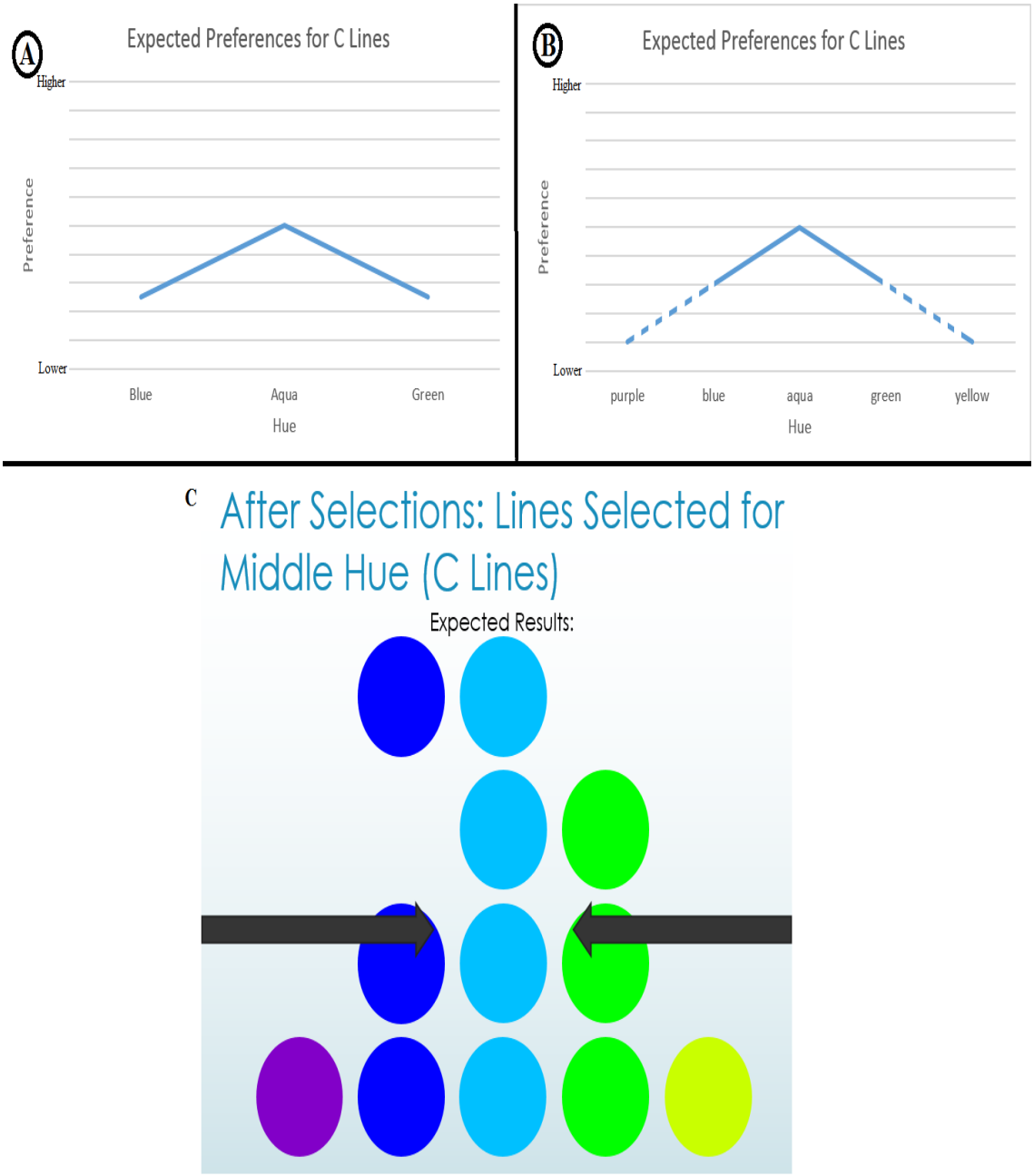


Figure 15: The Predicted Preferences for the C Lines After 22 Generations of Selection; *A) When the C Lines are introduced to two choice situations, B) This is a similar graph to (A), but with the five hue choices and their predicted preference values in the C lines. C) A colored representation of the preferences expected during the Assays*

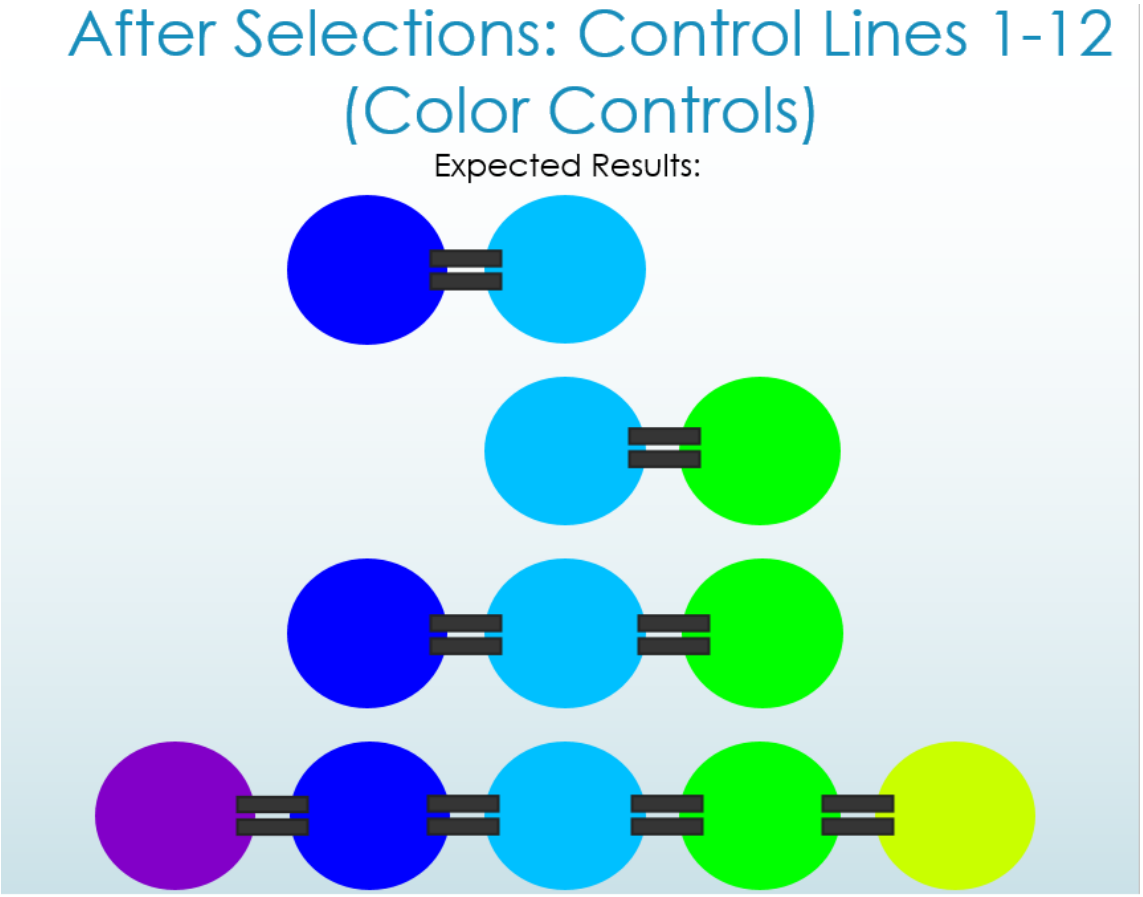
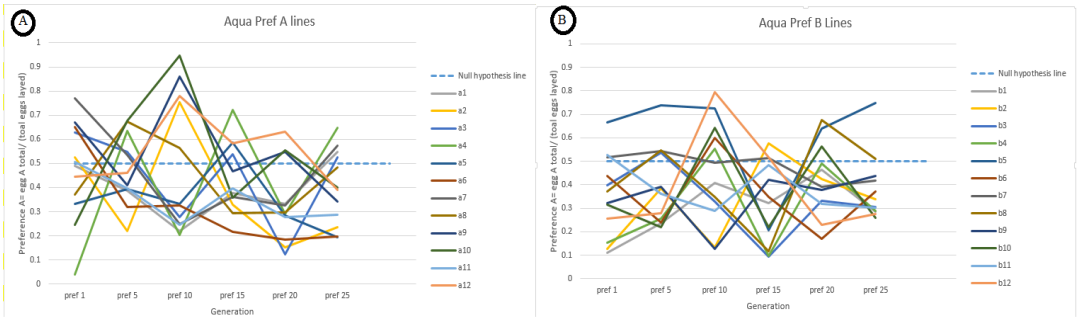
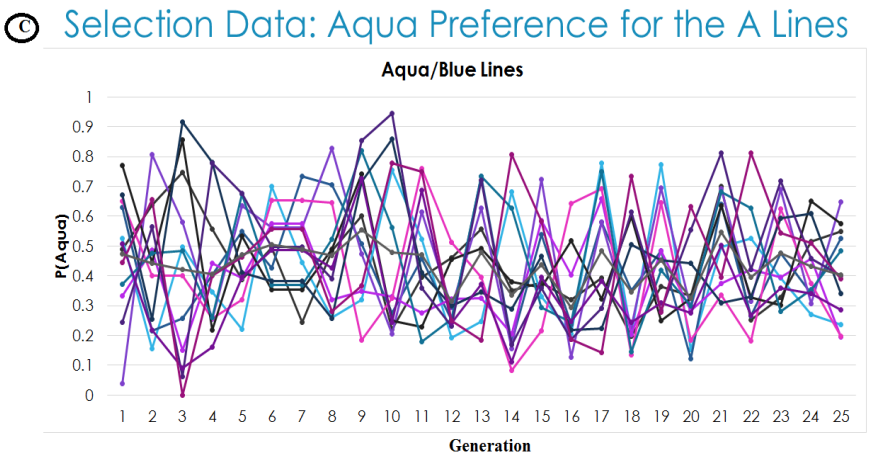


Figure 16: The Expected Preferences for the Color Controls during the Assay Trials.





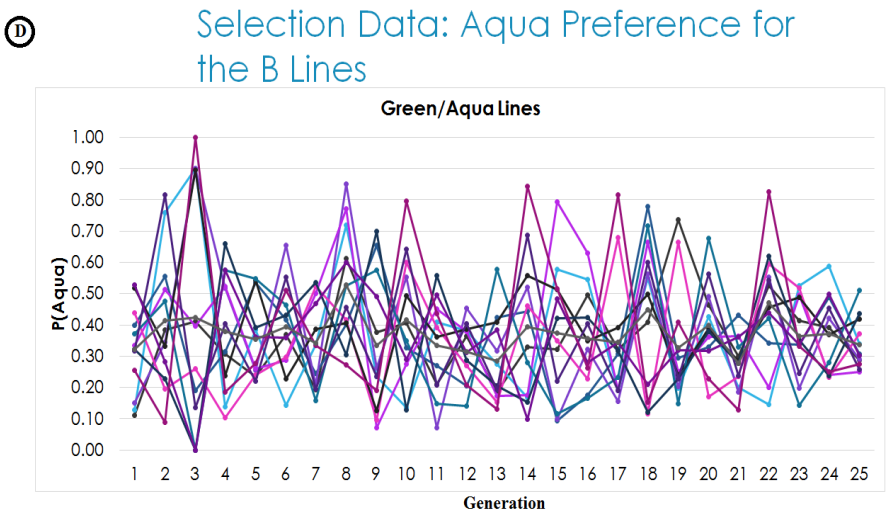


Figure 17: Preference for Aqua Hue for the A Lines and B Lines; *A-B) The preference for Aqua was determined by the equation: (Total Eggs Laid on Aqua)/ (Total Eggs Laid on all Hues). Each Replicate was graphed for the A and B Lines every five generations. The Dashed line represents the Null Hypothesis Line which estimated the Aqua Hue preference in a two-choice selection when no preference exists or evolves (0.5). C-D) all replicates graphed for every generation, graphed similar to (A & B).*

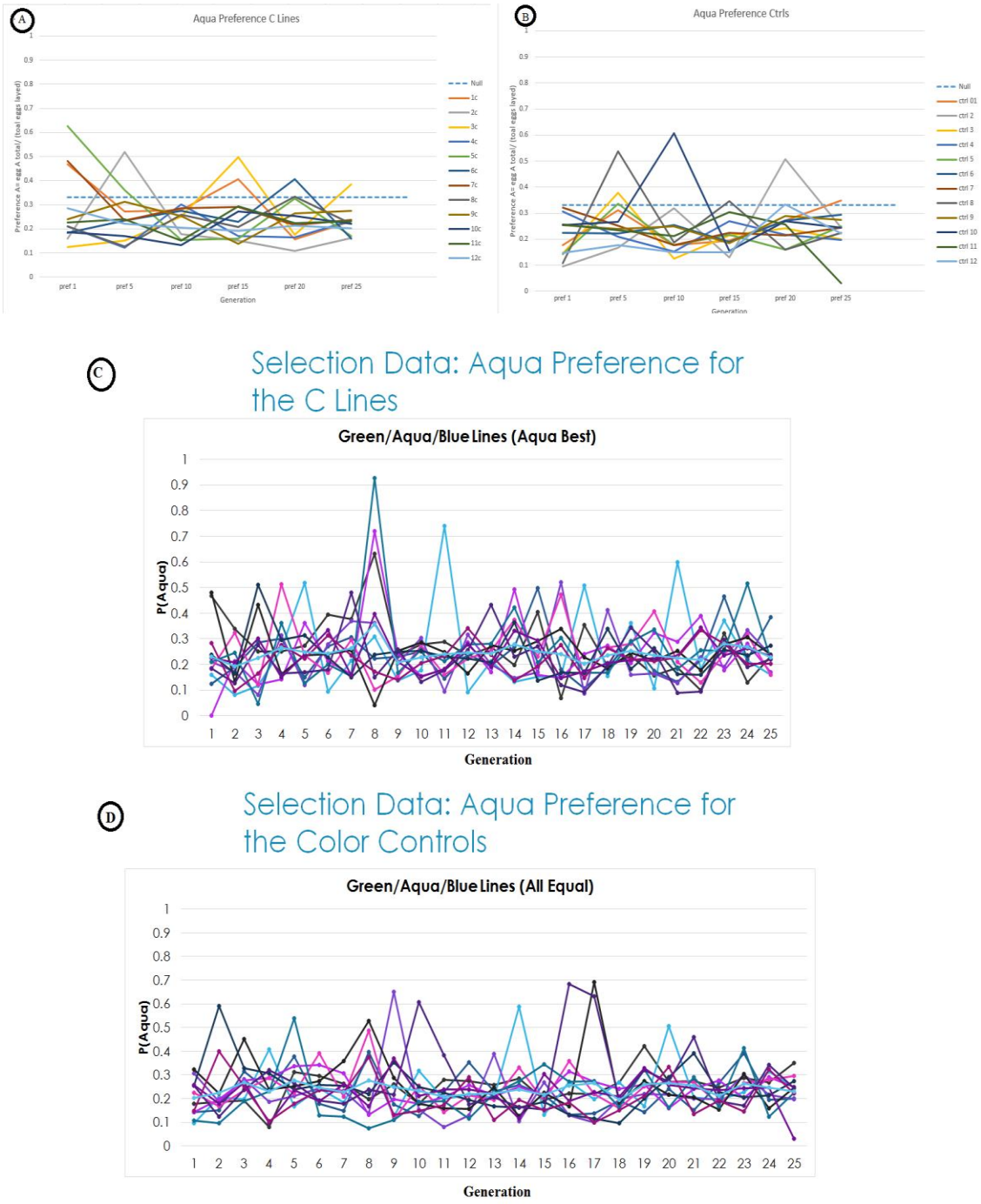


Figure 18: Preference for Aqua Hue for the C Lines and Color Controls; *A-B) The preference for Aqua was determined by the equation: (Total Eggs Laid on Aqua)/ (Total Eggs Laid on all Hues). Each Replicate was graphed for the C Lines and Color Controls every five generations. The Dashed line represents the Null Hypothesis Line which estimated the Aqua Hue preference in a three-choice selection when no preference exists or evolves (0.33). C-D) all replicates graphed for every generation, graphed similar to (A & B).*

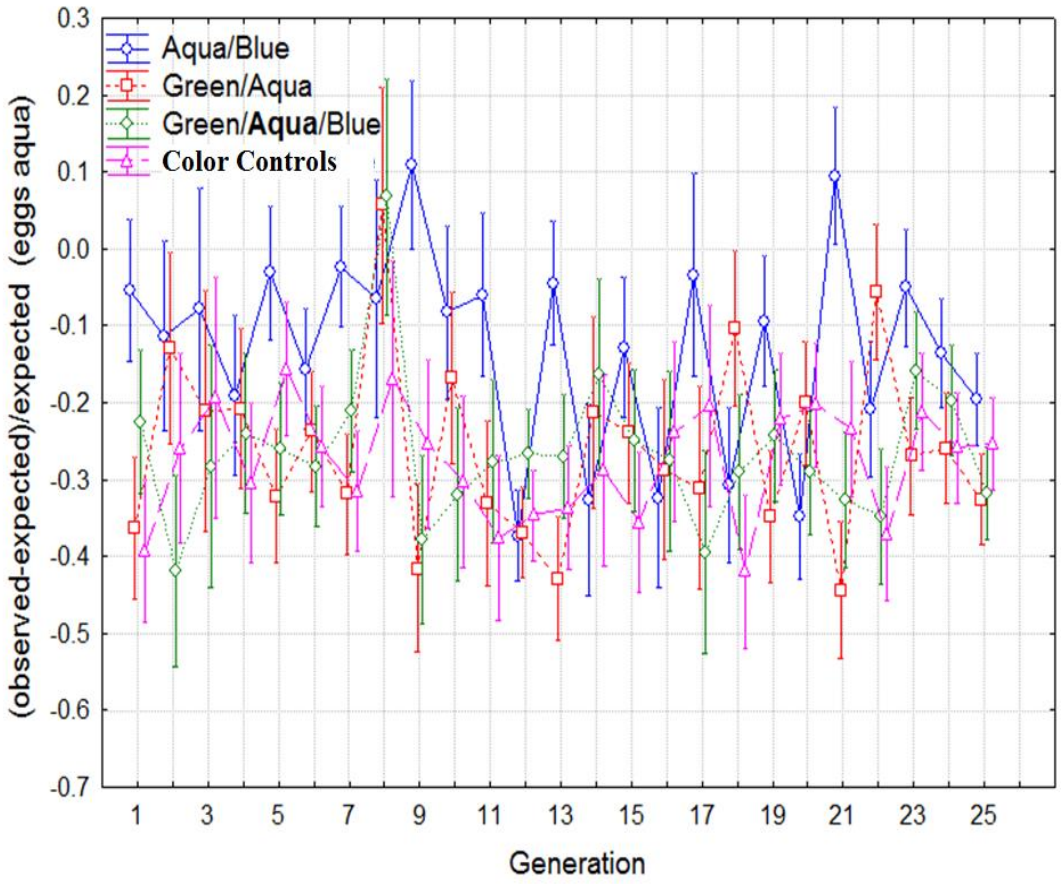


Figure 19: The (Observed-Expected)/(Expected) Egg Laying Preference= Aqua Preference per Generation

The Blue Line is the A Line Treatment group, the Red Line is the B Line Treatment group, the Green Line is the C Line Treatment group, and the Pink Line is the Color Controls. Each Line is the averaged Treatment of all the 12 replicate within the Treatment Group.

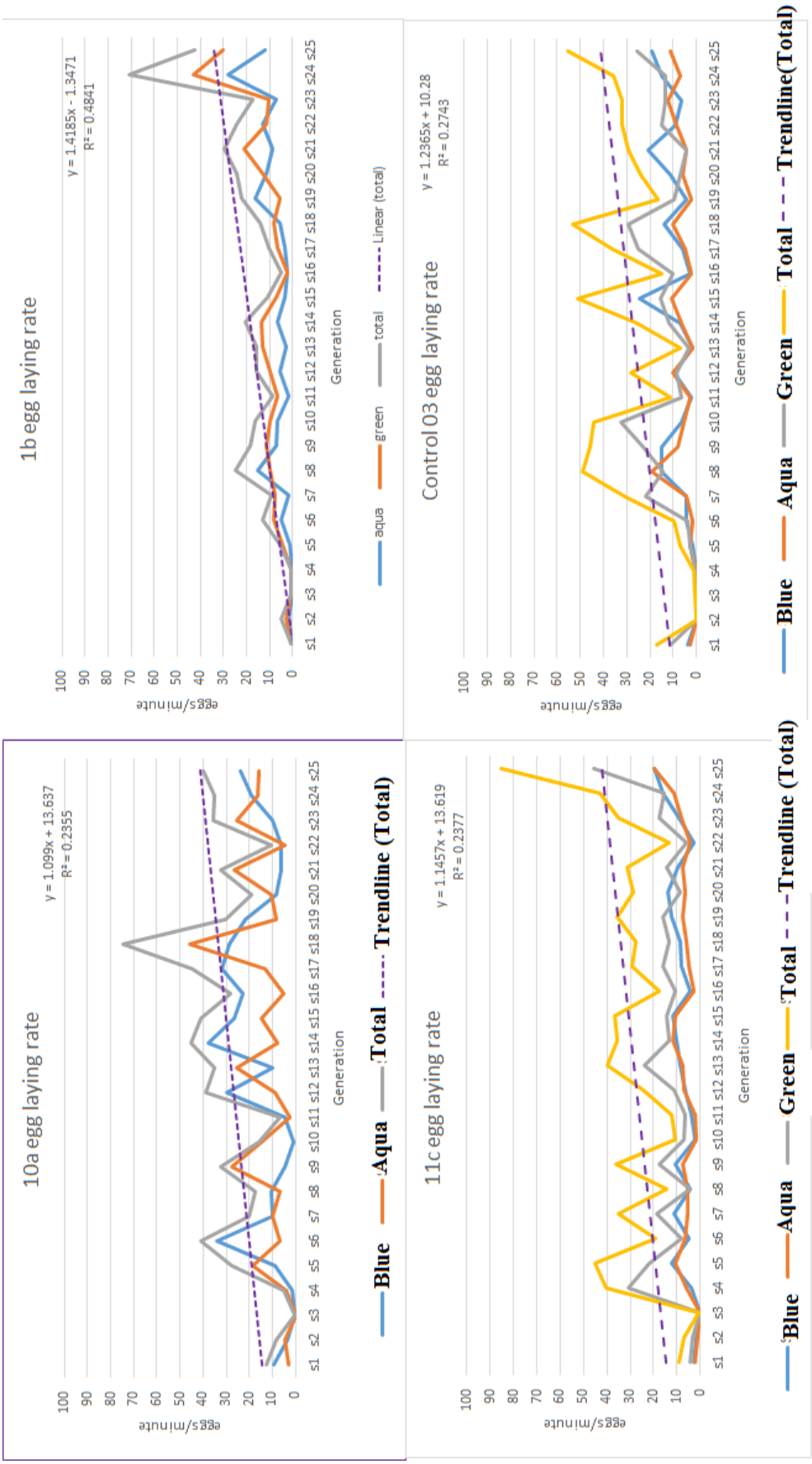


Figure 20: Examples of Egg Laying Rates over Selection Generations
Each Graph represents a single replicate of each Treatment type, and a Color Control, showing hte total eggs laid per minute on each hue, in total for all hues, and for each generation. The Trendline (dashed) in each graph shows the eggs/minute laid for all hues (total), and the liniar equation of this line is seen in the upper right hand corner of each graph. To see all of the egg laying rate graphs for all replicates see Appendix 5.

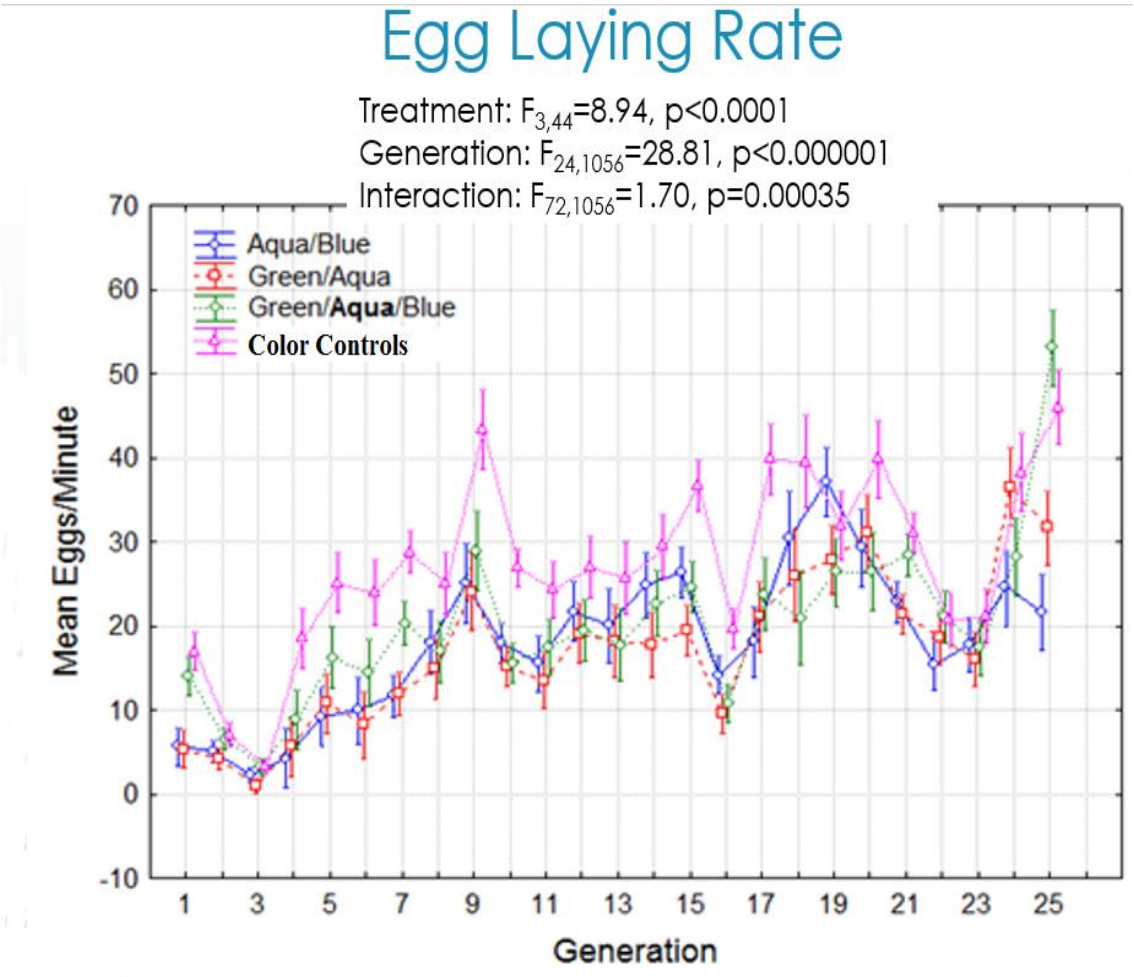


Figure 21: The Average Egg Laying Rate Per Generation
The combined replicates were averaged into a single line for each treatment group and the Color Controls. The A Lines are graphed in Blue, the B Lines graphed in Red, the C Lines graphed in Green, and the Color Controls graphed in Pink.

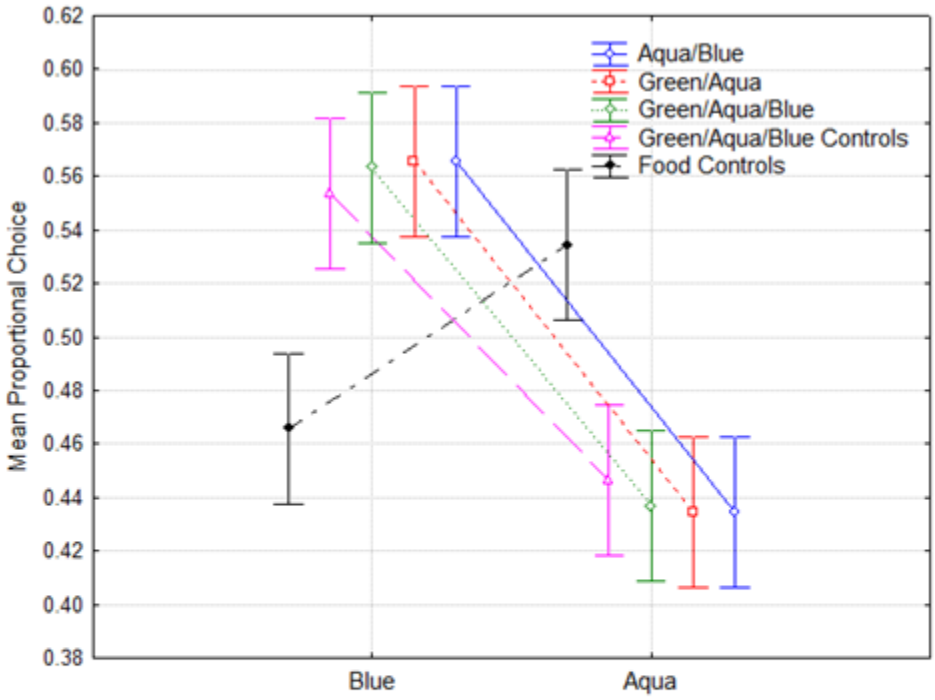


Figure 22:The Assays for the Two-Choice Blue vs. Aqua Hue Tests for all Treatment Types.
Each of the replicates and repeats were combined into an average treatment preference for each Hue disk offered in the experiment. The A lines are colored in Blue, the B lines in Red, the C lines in Green, the Color Controls in Pnk, and the Food Controls in Black.

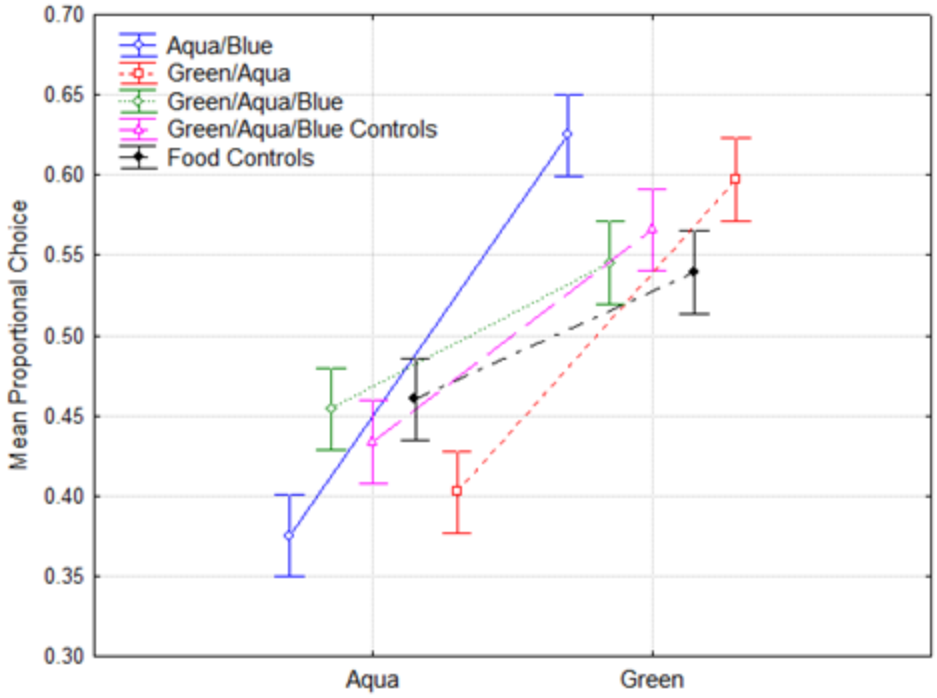


Figure 23: Assays for the Two-Choice Aqua vs Green Hue Tests

Each of the replicates and repeats were combined into an average treatment preference for each Hue disk offered in the experiment. The A lines are colored in Blue, the B lines in Red, the C lines in Green, the Color Controls in Pnk, and the Food Controls in Black.

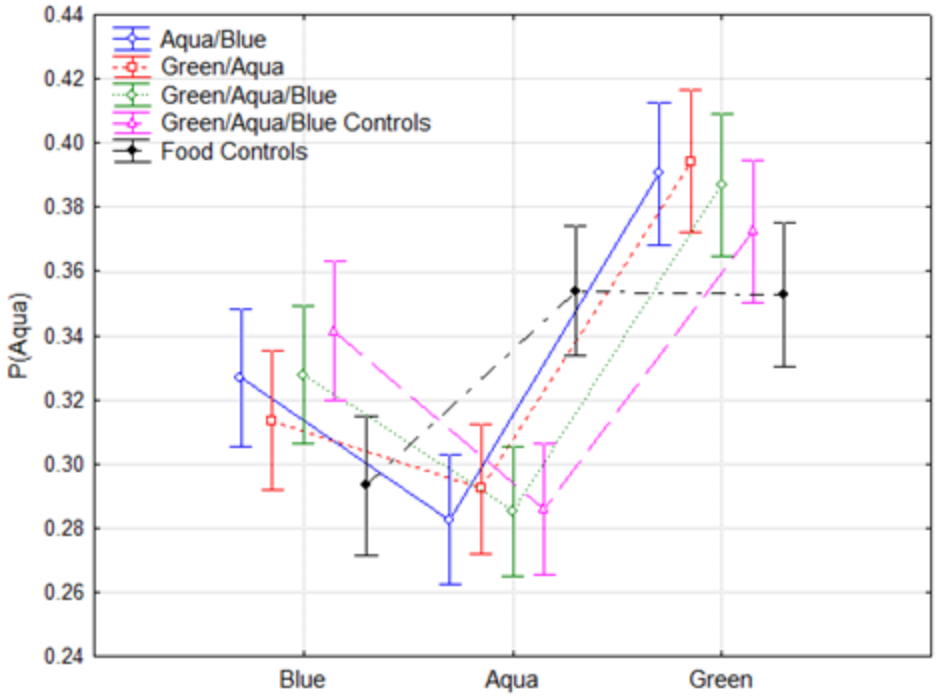


Figure 24: The Assays for the Three-Choice Blue vs. Aqua vs. Green Tests

Each of the replicates and repeats were combined into an average treatment preference for each Hue disk offered in the experiment. The A lines are colored in Blue, the B lines in Red, the C lines in Green, the Color Controls in Pnk, and the Food Controls in Black.

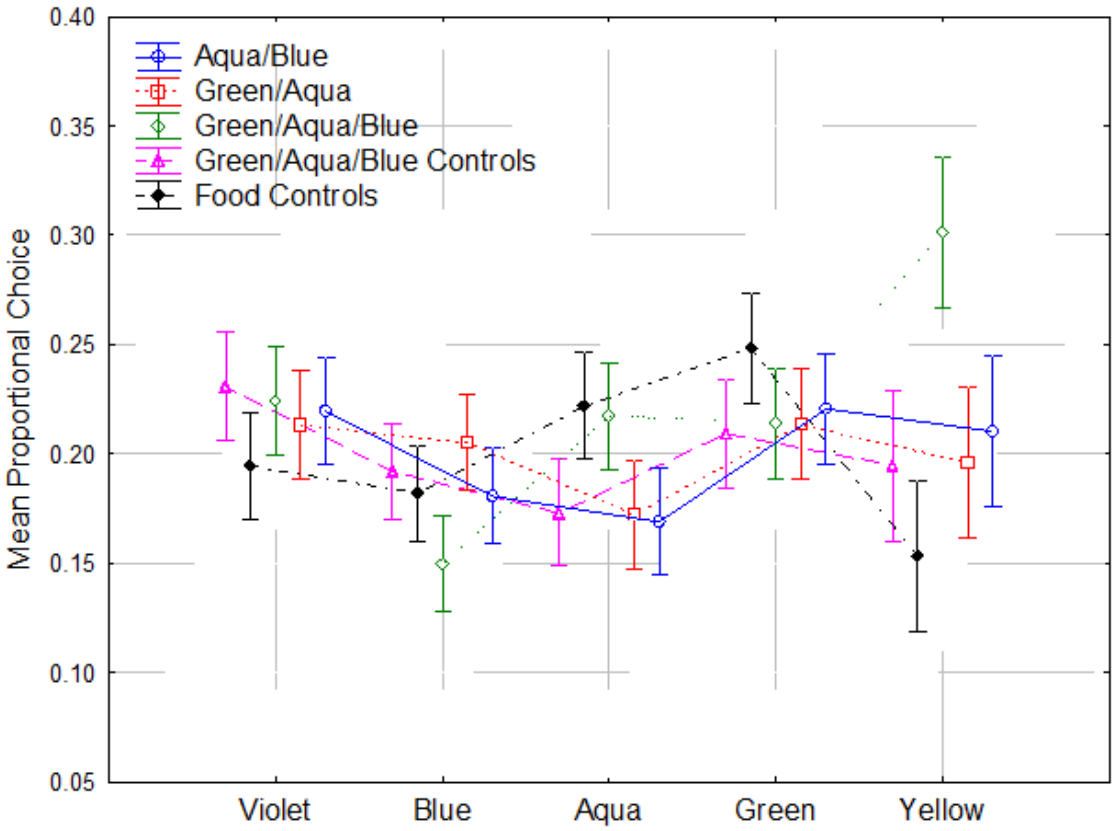


Figure 25: The 5-Hue-Choice Assay Test for All Treatment Types
The A lines are grpahed in blue, the B lines in red, the C lines in green, the Color Controls in pink , and the Food Controls in Black.

Appendix 1: Pre-Selection Methods & Data

The Laboratory Wild Type (FV) *Drosophila melanogaster* eggs were collected for discrimination conditioning (adverse) testing. Each line tested, was collected in six vials with standard fly food, each vial contained eighty eggs: for a total egg count of 480 eggs/flies per line.

The first experiment of discrimination testing was between the corresponding RGB hues of the wavelengths: 457.5 nm, 475 nm, and 492.5 nm. Each FV line was tested under one of nine conditioning/discrimination sets. All lines were introduced into separate cages with two Petri dishes with 50 ml of standard lab fly food. The cages were put into a climate chamber set at 24 °C, under Hitlights© LUMA10™ MULTICOLOR LED LIGHT STRIPS - SMD 5050 controlled LEDs set to cool white for three days, undisturbed. See Figure 7, and Appendix 1 Table 1.

Each line would be conditioned using [agar + quinine] mixture over the discriminated color disk, and a standard agar disk over the non-discriminated hue. Each line would be trained with the [quinine + agar] plates for 3 hours, the plates would be removed for 30 minutes, and new agar plates [no-quinine in any] would be introduced for 1.5 hours.

Under discrimination procedures, a line could be:

1) Conditioned against the hue 457.5 nm when paired with hue 475 nm.
2) Conditioned against the hue 475 nm when paired with hue 457.5 nm.
3) Conditioned against the hue 475 nm when paired with hue 492.5 nm.
4) Conditioned against the hue 492.5 nm when paired with hue 475 nm.

5) Conditioned against the hue 457.5 nm when paired with hue 492.5 nm.
6) Conditioned against the hue 492.5 nm when paired with hue 457.5 nm.

For comparison, there were three other sets that measured preferences of the FV lines to hue without conditioning:

7) Preference compared between hue 457.5 nm and hue 475 nm
8) Preference compared between hue 475 nm and hue 492.5 nm
9) Preference compared between hue 457.5 nm and hue 492.5 nm

Each set was run until 17 separate lines were tested under each set.

The second experiment of discrimination testing was between the corresponding RGB hues of the wavelengths: 440 nm, 475 nm, and 510 nm. This second experiment followed the same procedure as the first experiment, substituting the 440 nm hue for the 457.5 nm hue, and replacing the 492.5 nm hue with the 510 nm hue. These discrimination sets were run until 11 separate replicates were tested for each condition or preference.

All of the [no-quinine] plates were photographed, and the total eggs counted.

Results:

No obvious results from the data but see Appendix 1 Table 2 for further data. The greatest oddity is that in some of the discrimination testing, the hue color that had a quinine paired in the learning phase, that hue would have a greater number of eggs laid on it compared to a control test. As if the flies were using the quinine as an indication point of which hue to lay on. This was not constant.

Tables:

Appendix 1 Table 1: Wavelength to RGB-hue conversion Used in Experiments						
Wavelength (λ)	RGB Hexadecimal			The Single Letter Designations		
	R	G	B	Pre- Data	Selection	Assay
405 nm	130	0	200			V
440 nm	0	0	255	D	B	B
457.5 nm	0	108	255	A		
475 nm	0	192	255	B, E	A	A
492.5 nm	0	255	234	C		
510 nm	0	255	0	F	G	G
562.5 nm	201	255	0			Y

Appendix 1 Table 2:

Test Type	Q	Wavelength 457.5 eggs	Wavelength 475 eggs	Wavelength 492.5 eggs	Wavelength 440 eggs	Wavelength 475 eggs*	Wavelength 510 eggs	Total eggs	Pref (457.5)	Pref (475)	Pref (492.5)	Pref (440)	Pref (475)*	Pref (510)	Pref (457.5)-control	Pref (475)-Control	Pref (492.5)-control	Pref (440)-control	Pref (475)*-control	Pref (510)-control
1	457.5	4191	3744	0	0	0	0	7935	0.528166	0.471834	0	0	0	0	0.086724	-0.08672	0	0	0	0
1	475	3156	5010	0	0	0	0	8166	0.386481	0.613519	0	0	0	0	-0.05496	0.054962	0	0	0	0
1	control	7467	9448	0	0	0	0	16915	0.441443	0.558557	0	0	0	0	0	0	0	0	0	0
2	475	0	4346	8701	0	0	0	13047	0	0.333103	0.666897	0	0	0	0	-0.12593	0.125934	0	0	0
2	492.5	0	6619	6693	0	0	0	13312	0	0.497221	0.502779	0	0	0	0	0.038183	-0.03818	0	0	0
2	control	0	7637	9000	0	0	0	16637	0	0.459037	0.540963	0	0	0	0	0	0	0	0	0
3	457.5	5193	0	6068	0	0	0	11261	0.461149	0	0.538851	0	0	0	0.040131	0	-0.04013	0	0	0
3	492.5	6109	0	10403	0	0	0	16512	0.369973	0	0.630027	0	0	0	-0.05104	0	0.051045	0	0	0
3	control	5120	0	7041	0	0	0	12161	0.421018	0	0.578982	0	0	0	0	0	0	0	0	0
4	440	0	0	0	9256	9529	0	18785	0	0	0	0.492734	0.507266	0	0	0	0	-0.06532	0.06532	0
4	475	0	0	0	8483	8906	0	17389	0	0	0	0.487837	0.512163	0	0	0	0	-0.07022	0.070217	0
4	control	0	0	0	9084	7194	0	16278	0	0	0	0.558054	0.441946	0	0	0	0	0	0	0
5	475	0	0	0	0	4584	6740	11324	0	0	0	0	0.404804	0.595196	0	0	0	0	0.098396	-0.0984
5	510	0	0	0	0	6769	14658	21427	0	0	0	0	0.31591	0.68409	0	0	0	0	0.009502	-0.0095
5	control	0	0	0	0	4222	9557	13779	0	0	0	0	0.306408	0.693592	0	0	0	0	0	0
6	440	0	0	0	6659	0	13048	19707	0	0	0	0.3379	0	0.6621	0	0	0	-0.10052	0	0.100523
6	510	0	0	0	7118	0	13844	20962	0	0	0	0.339567	0	0.660433	0	0	0	-0.09886	0	0.098857
6	control	0	0	0	5874	0	7524	13398	0	0	0	0.438424	0	0.561576	0	0	0	0	0	0

*475 wavelength is in relation to Test Types 4, 5 and 6 only

Appendix 2: Food Preparation & Procedure

Fly Food Recipe:

Ingredients	Max Batch Size (1 ½ +20%)	% Composition	Block
Water (mL)	8000	54.33%	1
Agar (g)	164	1.1%	
Molasses (mL)	1060	7.2%	
Cornmeal (g)	1060	7.2%	2
Brewer's Yeast (g)	840	5.7%	
Water (mL)	3460	23.5%	
Tegosept (g)	23	-	3
Ethanol (mL)	80	0.5%	
Propionic Acid (mL)	40.1	0.3%	
Total (mL)	14,723.62		

1) Measure out Water and Agar from Block 1 and mix together in Large Soup Pot
2) Measure out Molasses in separate container

3) In third mixing pot measure out and combine all ingredients from Block 2. The longer this sits to mix the better. Cover and set aside.
4) In a 250 mL [G] glass beaker measure out the Tegosept, and set aside.
5) In separate [G] glass containers (usually Erlenmeyer Flasks are available), measure out the Ethanol and Propionic Acid.
6) Using a Balloon whisk that is large enough to not disappear in the Stock pot, keep the agar and water mixture suspended, and turn on the hot plate to setting 5 (out of 10).-Set the Heating Plate to setting 5. If setting 8 is used, the pot must be watched constantly.
7) Apply heat until temperature reaches 75 °C. Use an alcohol thermometer to measure the temperature.
8) Add molasses at 75 °C. If hot plate is not at setting 5, then set to 5. The Agar-Molasses-Water mixture must be constantly stirred to prevent the molasses burning.
9) Continue to heat to 80 °C –turn off the Hot plate to prevent molasses burning.
10) Pour the Cornmeal-Yeast-Water mixture into the Agar-Molasses-Water stock pot. Mix thoroughly.
11) Turn Hot plate back on to setting 5. *At this point the stock pot should be CONSTANTLY stirred, using the whisk to get into edges and keeping the ingredients suspended* Setting 8 can be used if the constant whisking is vigorous enough to prevent burning.
12) Continue stirring until 80 °C is reached again.

13) ~~P~~our the premeasured ethanol into ~~it~~ the glass beaker containing the Tegosept. The Tegosept should nearly instantly dissolve, and mixing it slightly will dissolve the remaining grains.
14) Once 80 °C is reached, add the ethanol-Tegosept mixture into the Stock pot *The Hot plate should remain at setting 5 from this point on*. Mix thoroughly.
15) Continuously and vigorously whisk the stock pot For 5 minutes should be, without stopping. (Two songs on the radio).
16) Turn off the hot plate and carefully remove the stock pot from hot plate.
17) Mix in the Propionic Acid to the stock pot.
18) Dispense food into determined containers. The food hardens within an hour. 6 mL per vial, 50 mL per Large Petri dish, and 50 mL per milk Bottle.

Agar Standard Recipe

Ingredients	100 mL
Water (mL)	100
Agar (g)	1
Sugar (g)	2

1) Measure out the ingredients in separate containers.
2) Heat water to boiling on hot plate or in microwave.
3) While stirring, add agar slowly to hot water.

4) Boil water-agar mixture until clear (I.e. Undissolved agar makes the mixture cloudy.)
5) Make sure the water level is the same as the original measured amount, add boiling water as necessary.
6) Using an alcohol thermometer, allow Agar mixture to cool to 70 °C, and then add in the measured sugar and stir well.
7) Dispense agar-sugar solution into containers within the next 30 minutes before it solidifies.
8) * This recipe can be extended. There is 1 g of Agar for every 100 mL of water, and 2 g of Sugar for every 100 mL of water.* Example: 600 mL water, 6 g Agar, 12 g Sugar.

Appendix 3: Example Data Table & Counting Sheet

Generational Data Sheets (Example)

Generation: _____ Date Run: _____ Time Start: _____ Time End: _____

Line	Hue 1	Petri Dish	Hue 2	Petri Dish	Hue 3	Petri Dish	Hue 4	Petri Dish	Hue 5	Petri Dish	Hue 6	Petri Dish
1A	X	X	A		A		B		B		X	X
2A	X	X	B		A		B		A		X	X
3A	X	X	B		B		A		A		X	X
4A	X	X	A		B		A		B		X	X
1B	X	X	G		G		A		A		X	X
2B	X	X	A		G		A		G		X	X
3B	X	X	G		A		G		A		X	X
4B	X	X	A		A		G		G		X	X
1C	B		A		G		B		A		G	
2C	B		G		A		B		G		A	
3C	G		A		B		G		A		B	
4C	G		B		A		G		B		A	
CTRL 1	A		B		G		A		B		G	
CTRL 2	A		G		B		A		G		B	

CTRL 3	G		B		A		G		B		A	
CTRL 4	A		B		G		A		B		G	
CTRL 13	X	X	X	X	X	X	X	X	X	X	X	X
CTRL 14	X	X	X	X	X	X	X	X	X	X	X	X
CTRL 15	X	X	X	X	X	X	X	X	X	X	X	X
CTRL 16	X	X	X	X	X	X	X	X	X	X	X	X

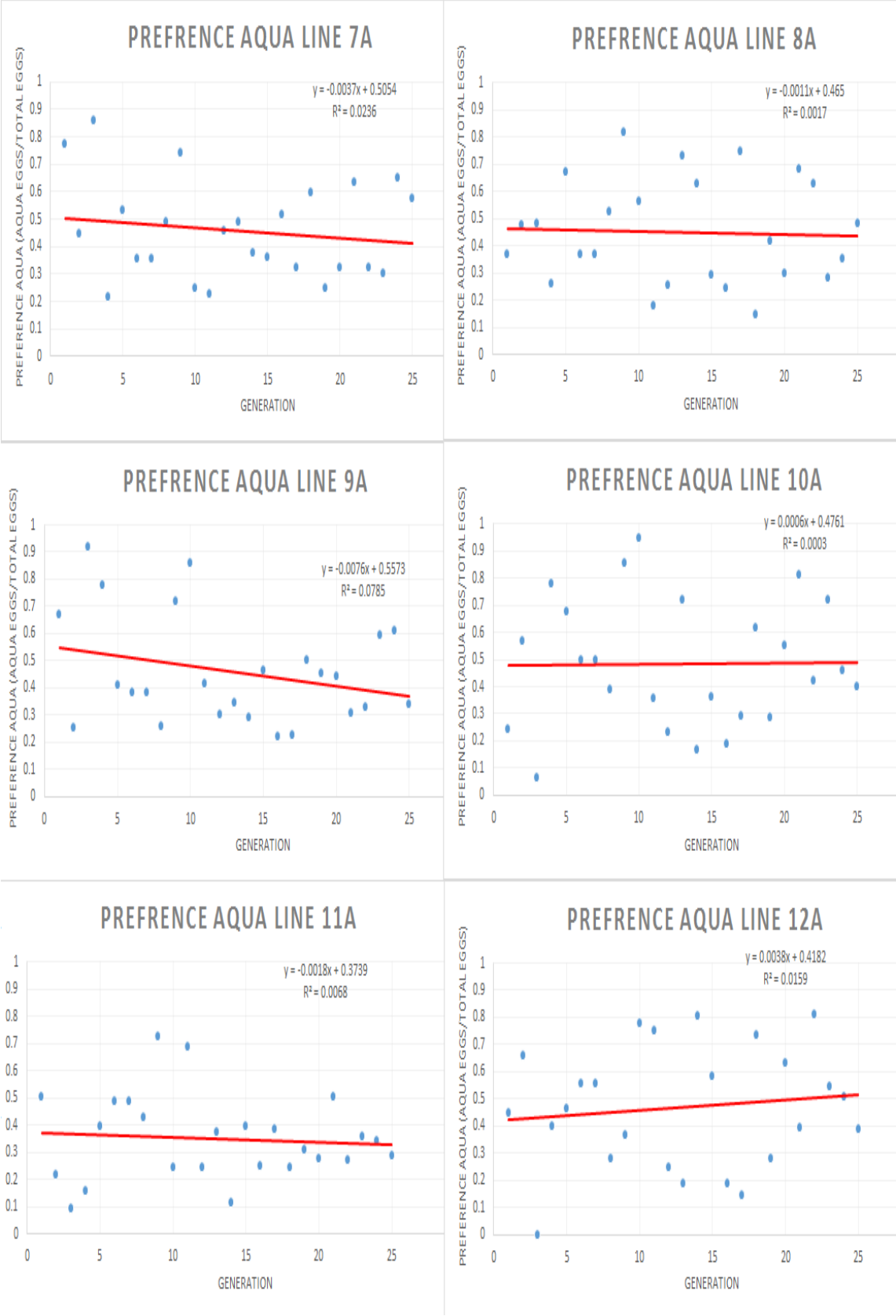
Counting Data Sheet (Example)

Generation Date: _____

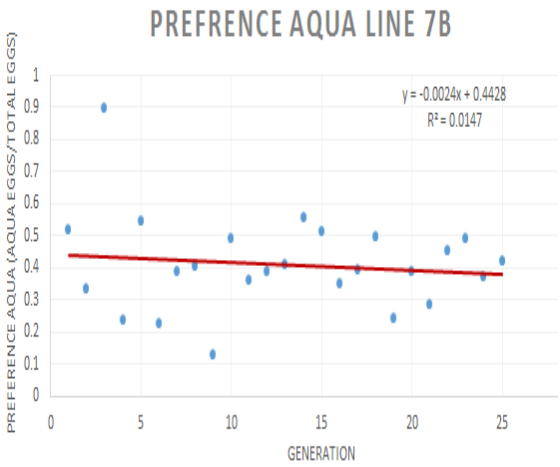
Petri Dish Id.			Egg totals	Hue	Hue Totals	Notes
Location in Cage	Petri Dish Number	Photo Number				
1	xxxx	1		A	B=	

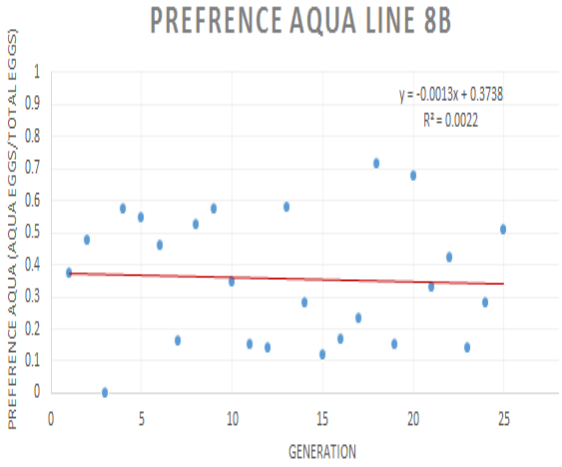
2	xxxx	1		A		
3	xxxx	1		B	A=	
4	xxxx	1		B		

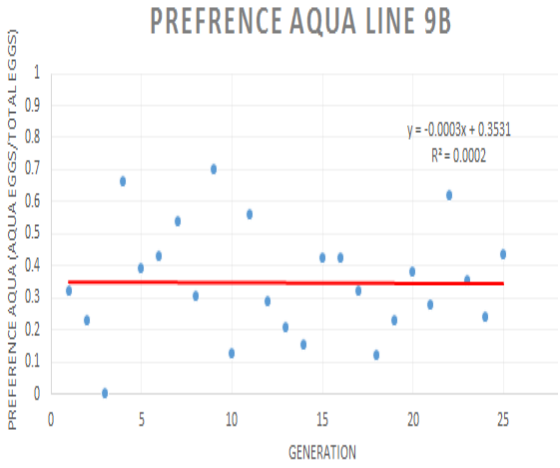
Appendix 4: Selection Preference Graphs

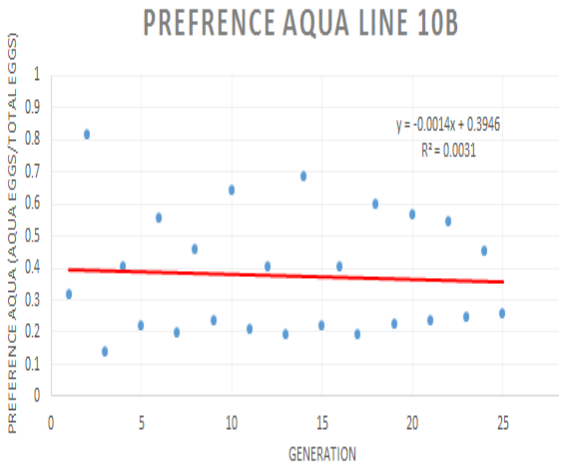

PREFRENCE AQUA LINE 7A
y = -0.0037x + 0.5054
R² = 0.0236
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 8A
y = -0.0011x + 0.465
R² = 0.0017
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 9A
y = -0.0076x + 0.5573
R² = 0.0785
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 10A
y = 0.0006x + 0.4761
R² = 0.0003
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 11A
y = -0.0018x + 0.3739
R² = 0.0068
GENERATION
PREFRENCE AQUA LINE 12A
y = 0.0038x + 0.4182
R² = 0.0159
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION

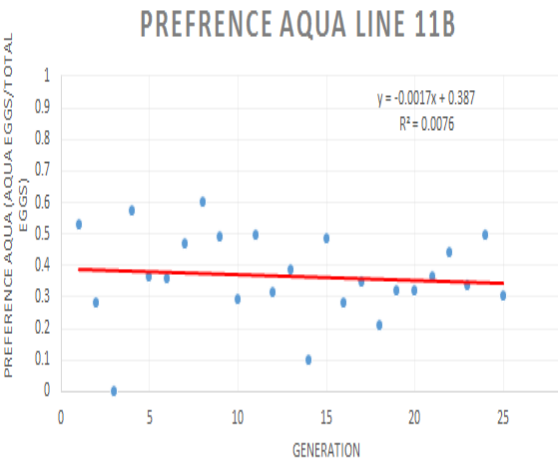

PREFRENCE AQUA LINE 1B
y = 0.006x + 0.2884
R² = 0.1057
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 2B
y = -0.0023x + 0.4062
R² = 0.0062
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 3B
y = -0.0011x + 0.3846
R² = 0.0026
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 4B
y = -0.0065x + 0.4656
R² = 0.0461
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 5B
y = -0.0035x + 0.4283
R² = 0.0185
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION
PREFRENCE AQUA LINE 6B
y = 0.0048x + 0.2813
R² = 0.0402
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION

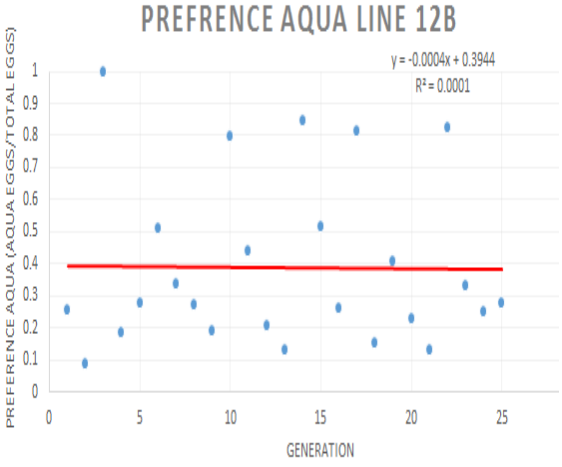

PREFRENCE AQUA LINE 7B
y = -0.0024x + 0.4428
R² = 0.0147
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION

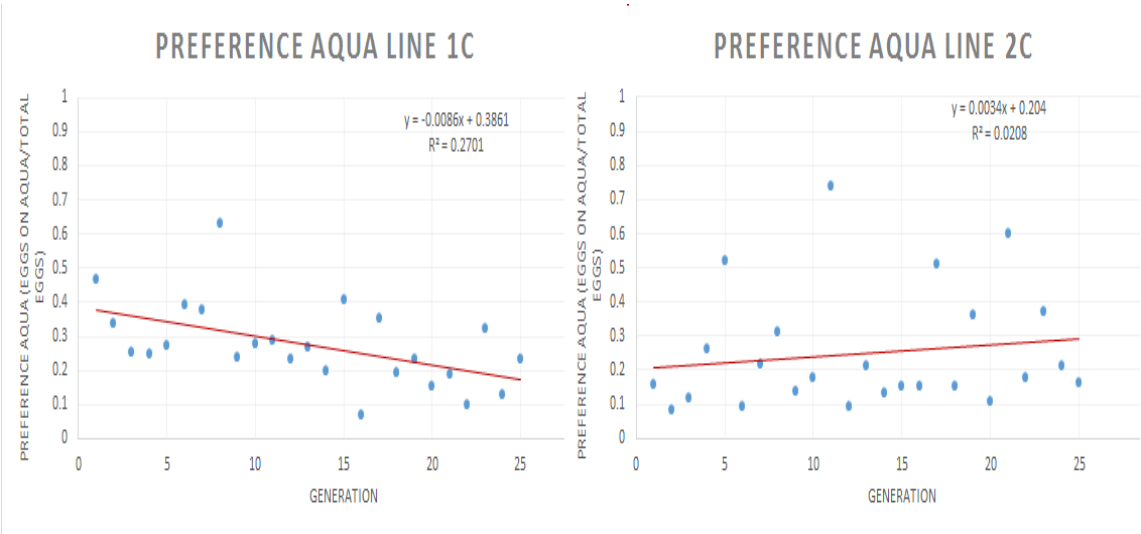

PREFRENCE AQUA LINE 8B
y = -0.0013x + 0.3738
R² = 0.0022
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION


PREFRENCE AQUA LINE 9B
y = -0.0003x + 0.3531
R² = 0.0002
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION

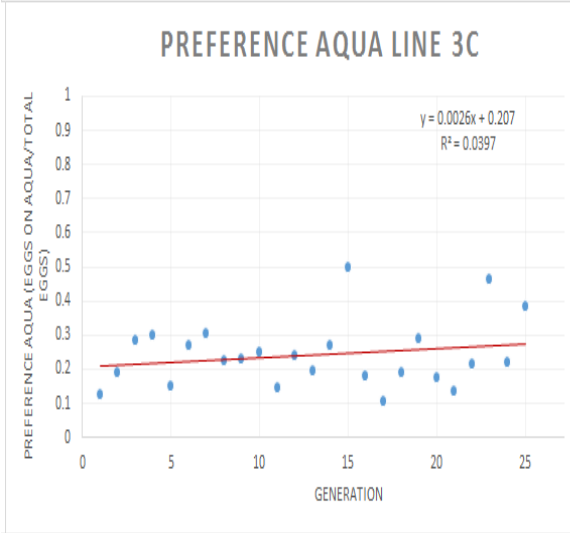

PREFRENCE AQUA LINE 10B
y = -0.0014x + 0.3946
R² = 0.0031
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION

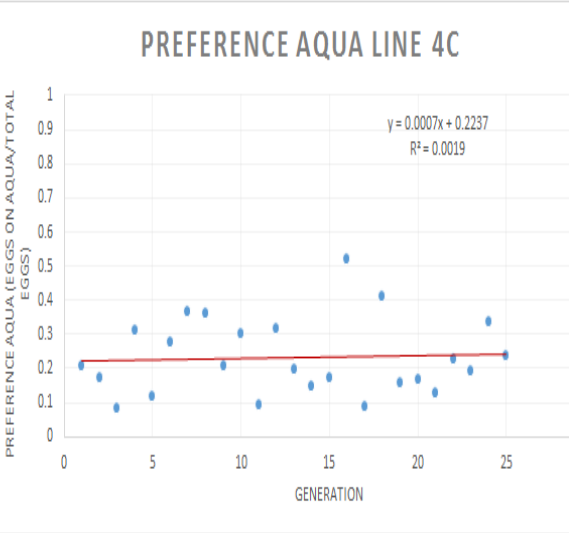

PREFRENCE AQUA LINE 11B
y = -0.0017x + 0.387
R² = 0.0076
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION

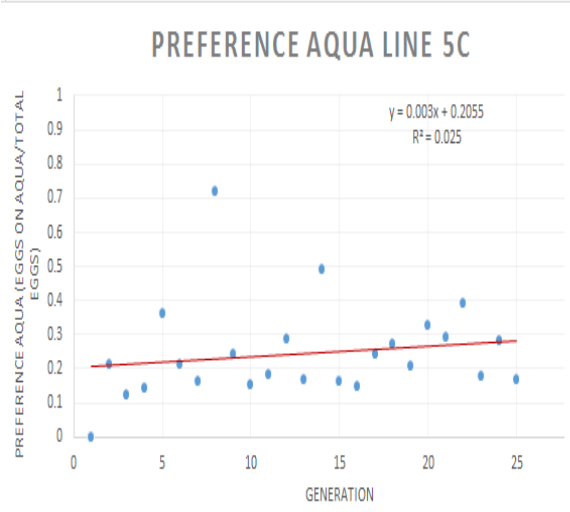

PREFRENCE AQUA LINE 12B
y = -0.0004x + 0.3944
R² = 0.0001
PREFERENCE AQUA (AQUA EGGS/TOTAL EGGS)
GENERATION

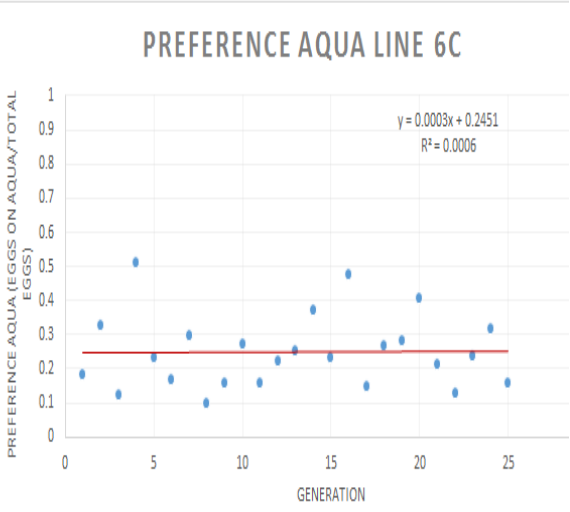

PREFERENCE AQUA LINE 1C
y = -0.0086x + 0.3861
R² = 0.2701
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

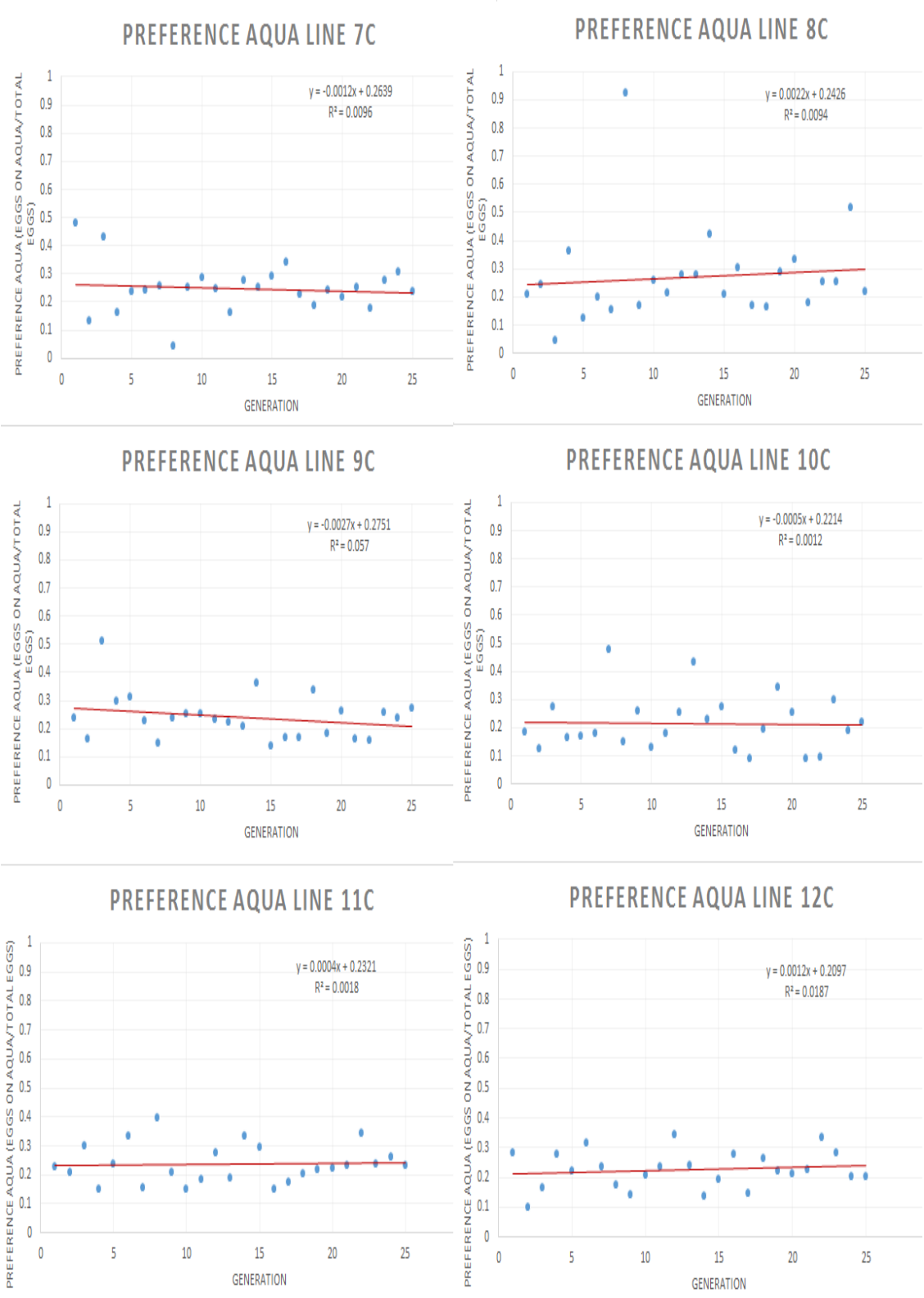
PREFERENCE AQUA LINE 2C
y = 0.0034x + 0.204
R² = 0.0208
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

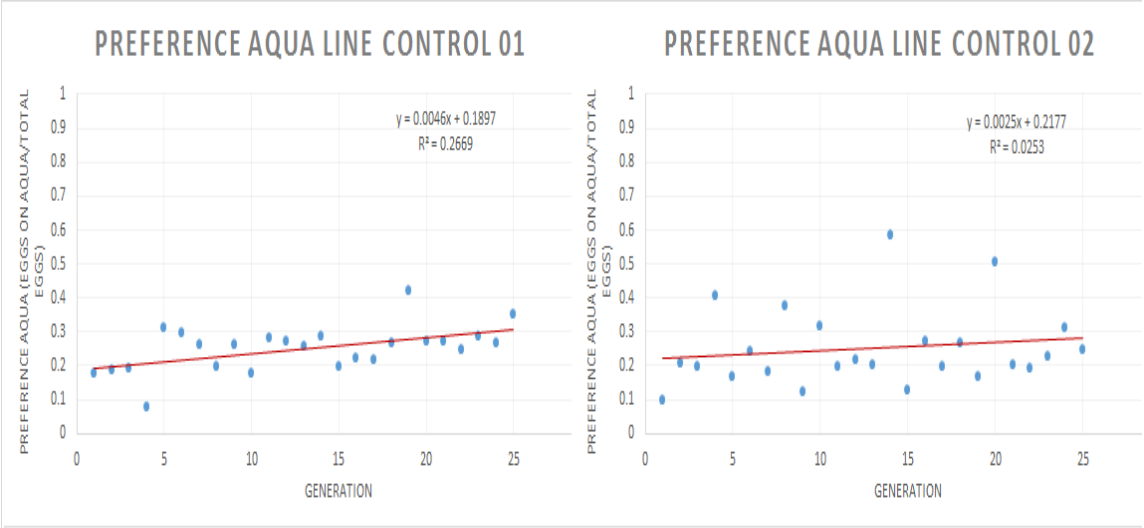

PREFERENCE AQUA LINE 3C
y = 0.0026x + 0.207
R² = 0.0397
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION


PREFERENCE AQUA LINE 4C
y = 0.0007x + 0.2237
R² = 0.0019
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

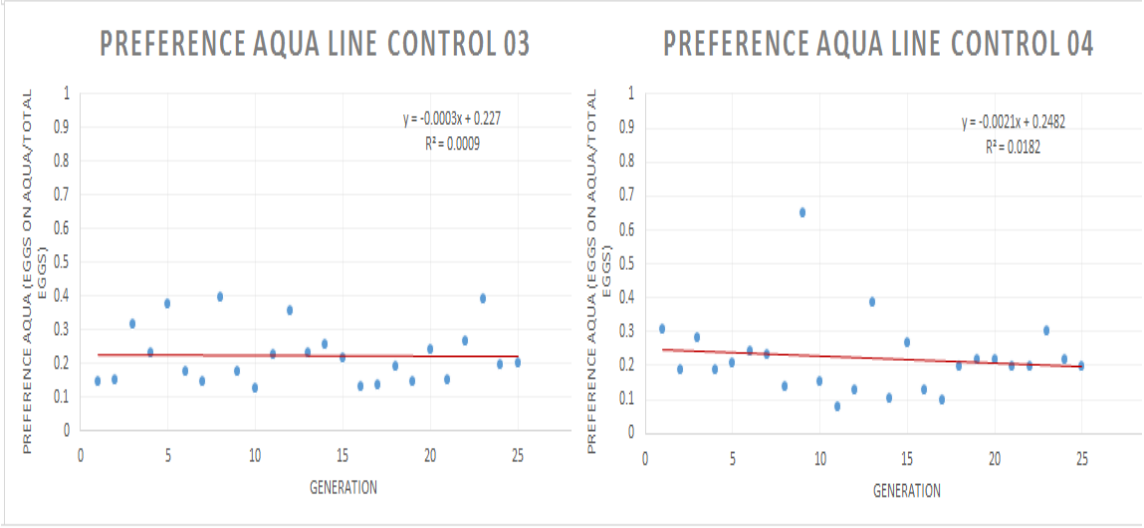

PREFERENCE AQUA LINE 5C
y = 0.003x + 0.2055
R² = 0.025
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION


PREFERENCE AQUA LINE 6C
y = 0.0003x + 0.2451
R² = 0.0006
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

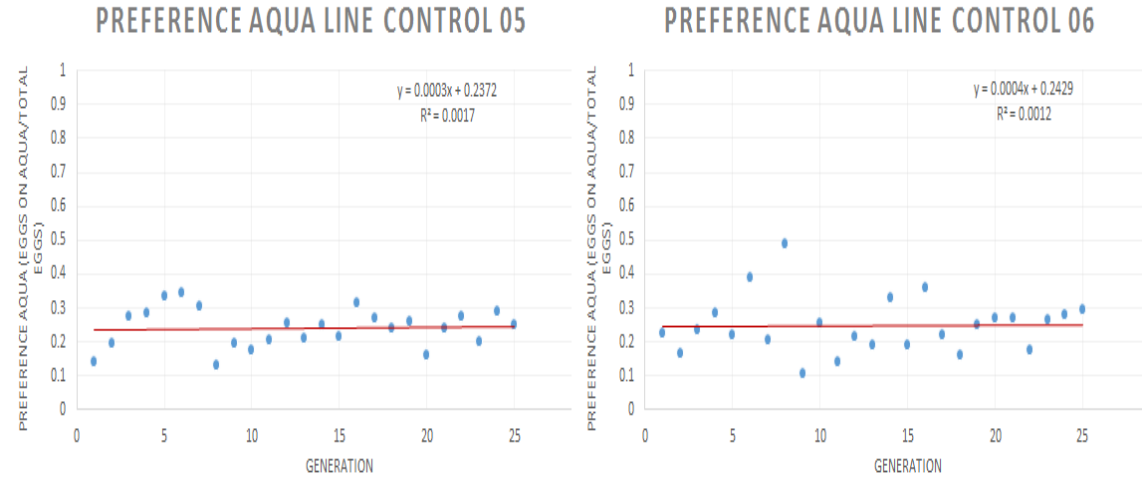

PREFERENCE AQUA LINE 7C
y = -0.0012x + 0.2639
R² = 0.0096
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE 8C
y = 0.0022x + 0.2426
R² = 0.0094
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE 9C
y = -0.0027x + 0.2751
R² = 0.057
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE 10C
y = -0.0005x + 0.2214
R² = 0.0012
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE 11C
y = 0.0004x + 0.2321
R² = 0.0018
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE 12C
y = 0.0012x + 0.2097
R² = 0.0187
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION


PREFERENCE AQUA LINE CONTROL 01
y = 0.0046x + 0.1897
R² = 0.2669
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

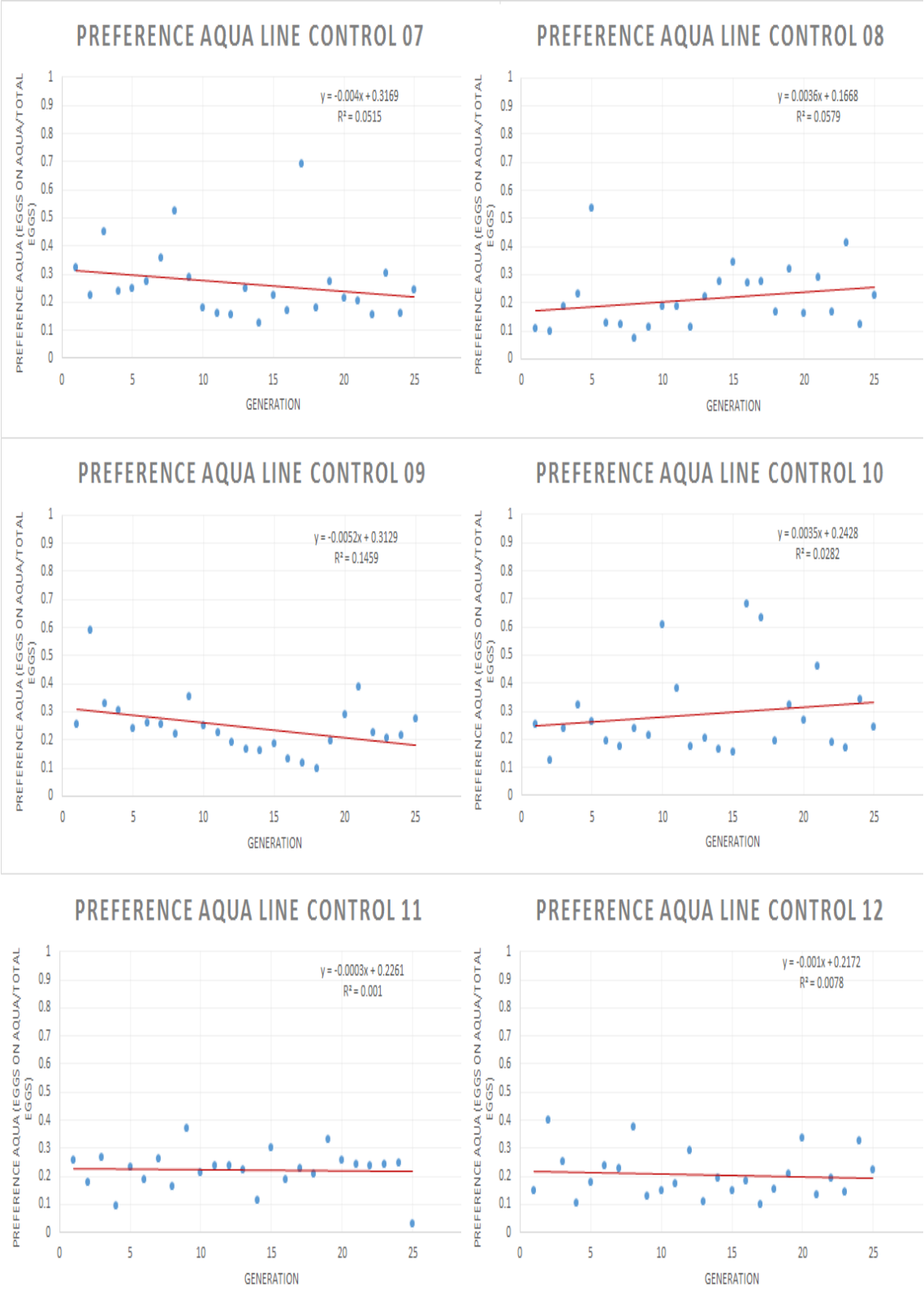
PREFERENCE AQUA LINE CONTROL 02
y = 0.0025x + 0.2177
R² = 0.0253
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

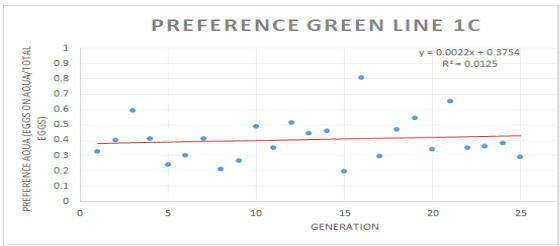

PREFERENCE AQUA LINE CONTROL 03
y = -0.0003x + 0.227
R² = 0.0009
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

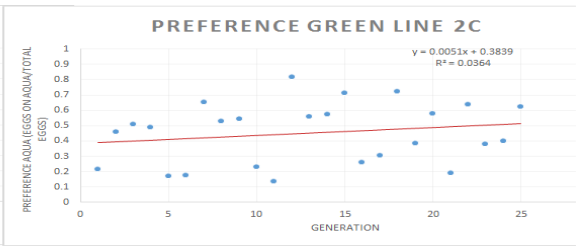
PREFERENCE AQUA LINE CONTROL 04
y = -0.0021x + 0.2482
R² = 0.0182
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

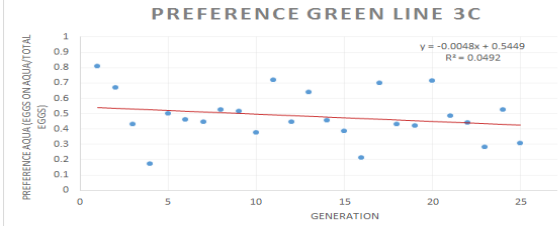

PREFERENCE AQUA LINE CONTROL 05
y = 0.0003x + 0.2372
R² = 0.0017
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

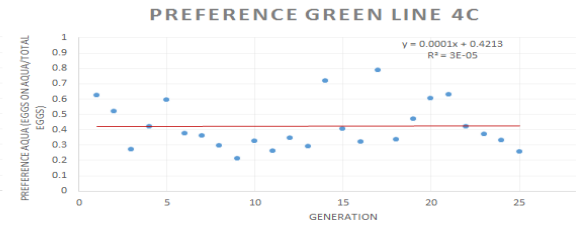
PREFERENCE AQUA LINE CONTROL 06
y = 0.0004x + 0.2429
R² = 0.0012
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

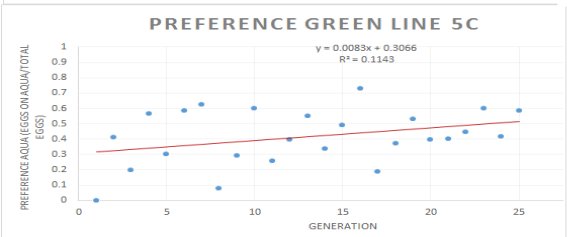

PREFERENCE AQUA LINE CONTROL 07
y = -0.004x + 0.3169
R² = 0.0515
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE CONTROL 08
y = 0.0036x + 0.1668
R² = 0.0579
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE CONTROL 09
y = -0.0052x + 0.3129
R² = 0.1459
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE CONTROL 10
y = 0.0035x + 0.2428
R² = 0.0282
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE CONTROL 11
y = -0.0003x + 0.2261
R² = 0.001
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION
PREFERENCE AQUA LINE CONTROL 12
y = -0.001x + 0.2172
R² = 0.0078
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

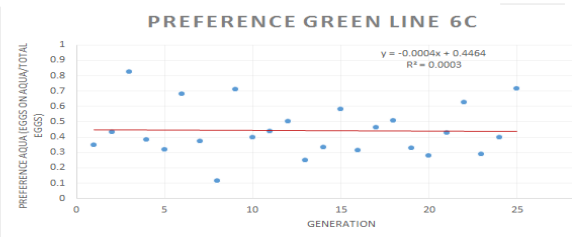

PREFERENCE GREEN LINE 1C
y = 0.0022x + 0.3754
R² = 0.0125
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

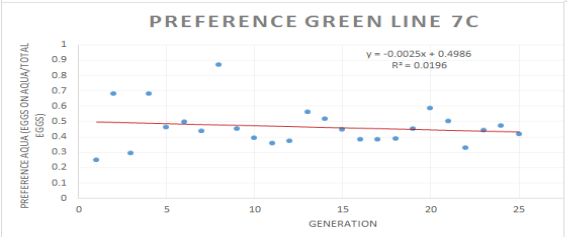

PREFERENCE GREEN LINE 2C
y = 0.0051x + 0.3839
R² = 0.0364
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

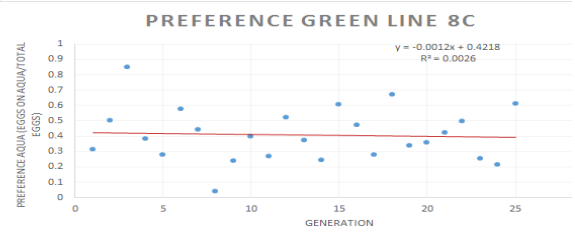

PREFERENCE GREEN LINE 3C
y = -0.0048x + 0.5449
R² = 0.0492
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

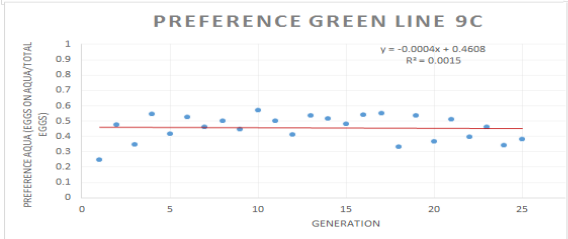

PREFERENCE GREEN LINE 4C
y = 0.0001x + 0.4213
R² = 3E-05
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

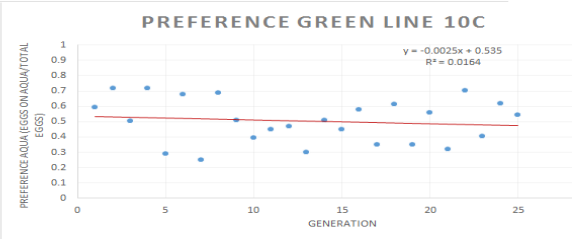

PREFERENCE GREEN LINE 5C
y = 0.0083x + 0.3066
R² = 0.1143
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

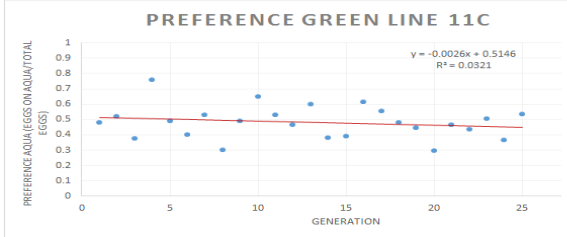

PREFERENCE GREEN LINE 6C
y = -0.0004x + 0.4464
R² = 0.0003
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

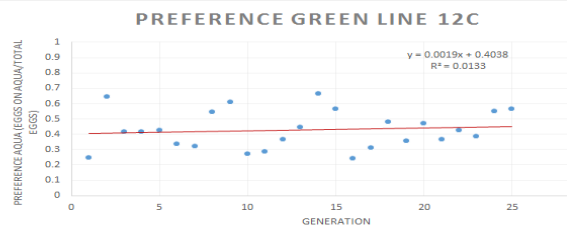

PREFERENCE GREEN LINE 7C
y = -0.0025x + 0.4986
R² = 0.0196
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

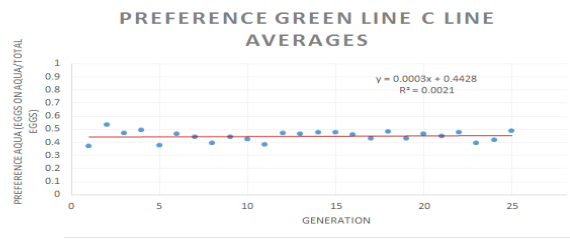

PREFERENCE GREEN LINE 8C
y = -0.0012x + 0.4218
R² = 0.0026
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION


PREFERENCE GREEN LINE 9C
y = -0.0004x + 0.4608
R² = 0.0015
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

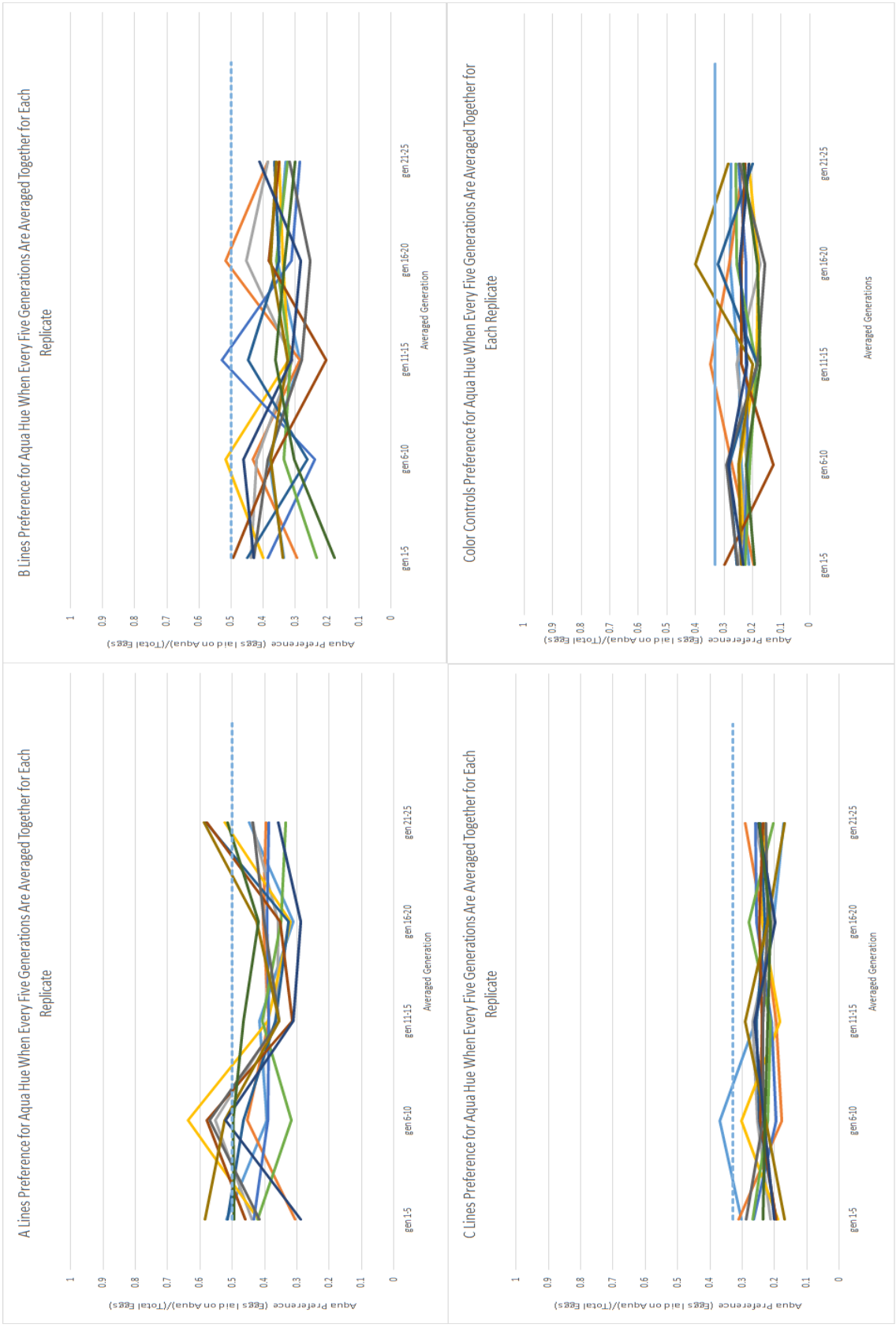

PREFERENCE GREEN LINE 10C
y = -0.0025x + 0.535
R² = 0.0164
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION


PREFERENCE GREEN LINE 11C
y = -0.0026x + 0.5146
R² = 0.0321
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

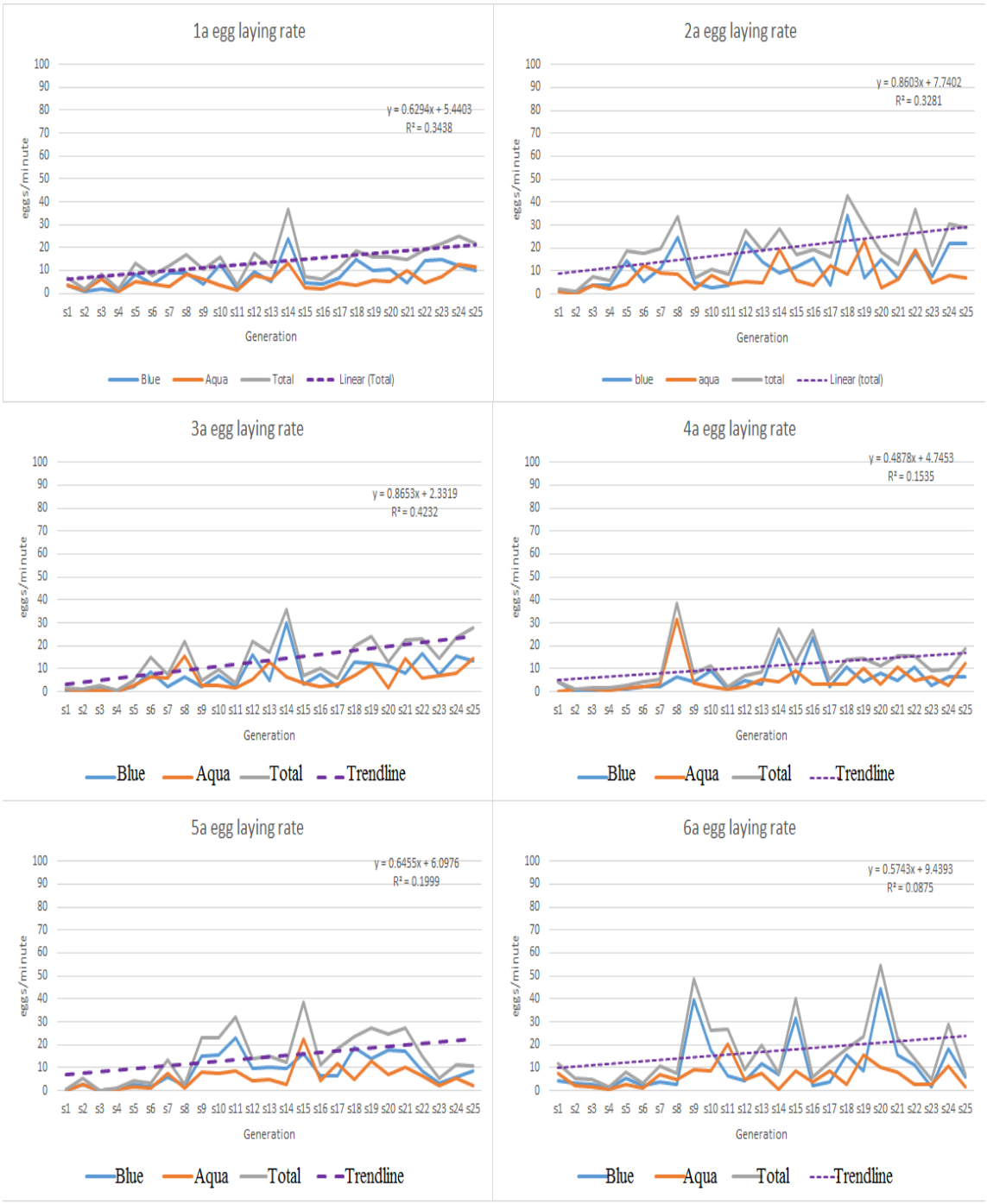

PREFERENCE GREEN LINE 12C
y = 0.0019x + 0.4038
R² = 0.0133
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

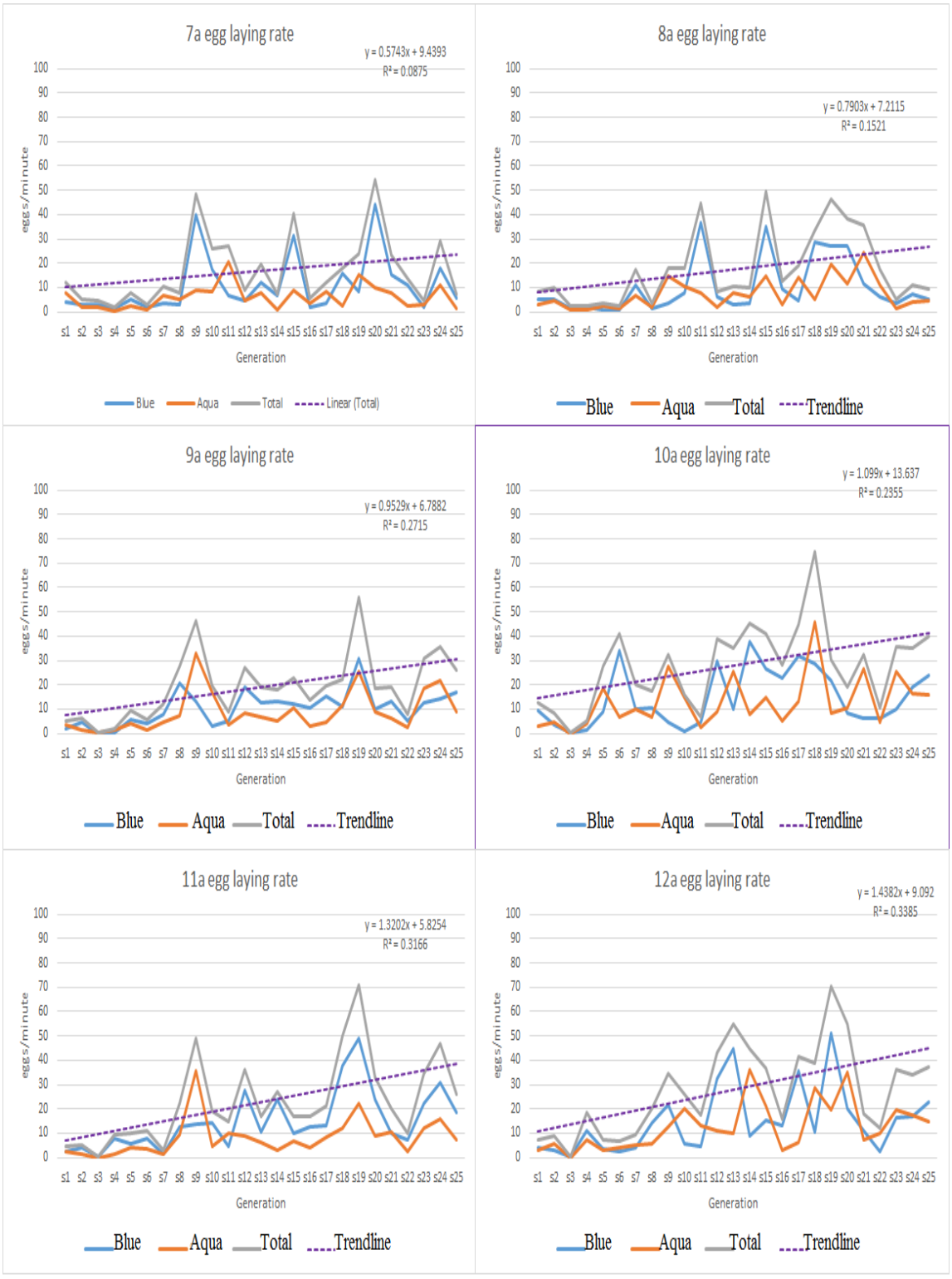

PREFERENCE GREEN LINE C LINE AVERAGES
y = 0.0003x + 0.4428
R² = 0.0021
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

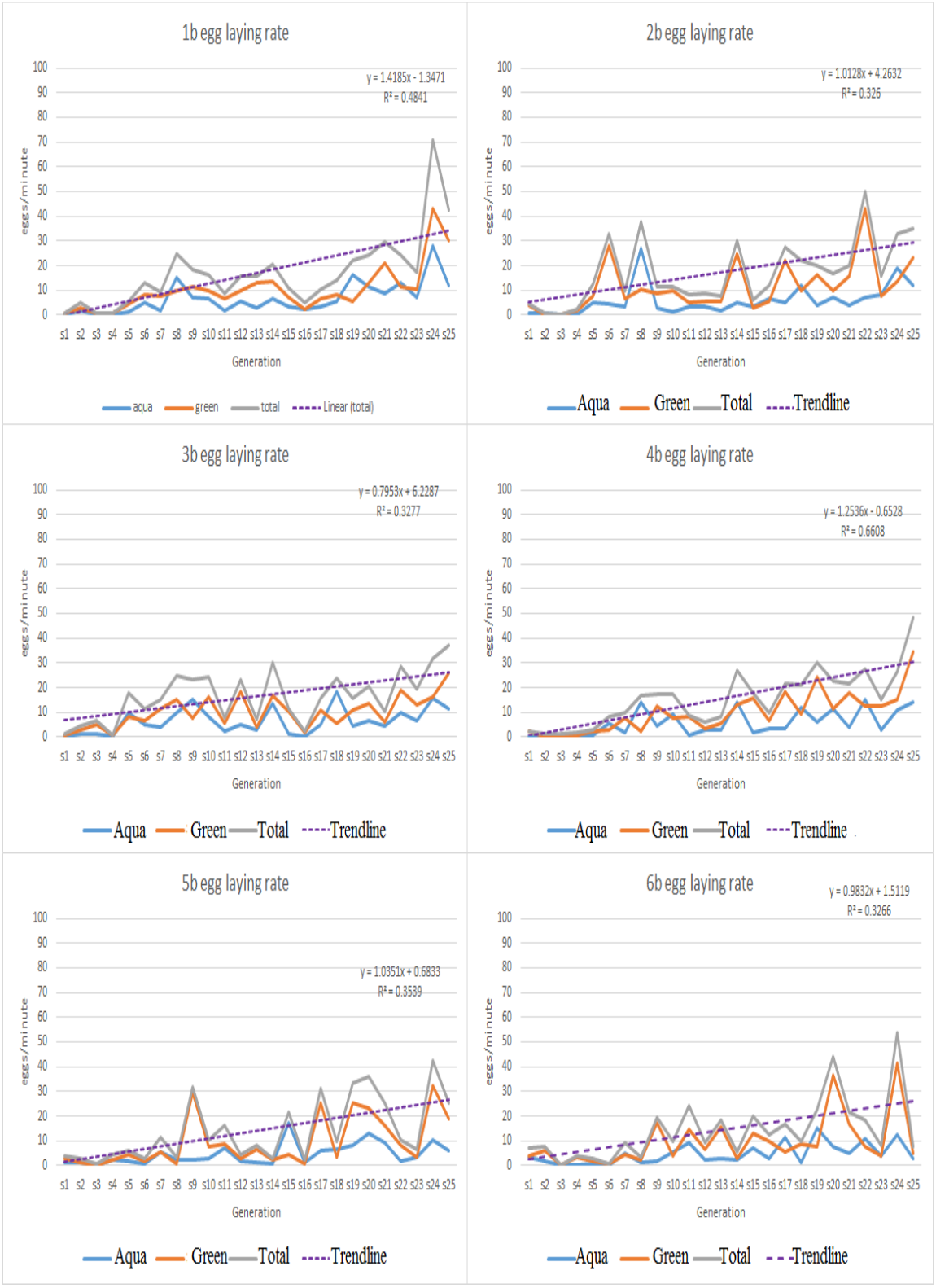

PREFERENCE GREEN CONTROL 01
y = -0.0058x + 0.5436
R² = 0.0703
PREFERENCE GREEN CONTROL 02
y = -0.0049x + 0.5103
R² = 0.0519
PREFERENCE GREEN CONTROL 03
y = -0.0042x + 0.5307
R² = 0.0386
PREFERENCE GREEN CONTROL 04
y = 0.0024x + 0.4857
R² = 0.0109
PREFERENCE GREEN CONTROL 05
y = -3E-06x + 0.4419
R² = 3E-08
PREFERENCE GREEN CONTROL 06
y = -0.0005x + 0.4523
R² = 0.0005
PREFERENCE GREEN CONTROL 07
y = -2E-05x + 0.4086
R² = 1E-06
PREFERENCE GREEN CONTROL 08
y = -0.0049x + 0.5818
R² = 0.0311
PREFERENCE GREEN CONTROL 09
y = 0.0067x + 0.3835
R² = 0.1104
PREFERENCE GREEN CONTROL 10
y = -0.0013x + 0.4575
R² = 0.0037
PREFERENCE GREEN CONTROL 11
y = 0.0018x + 0.4055
R² = 0.0193
PREFERENCE GREEN CONTROL 12
y = -4E-05x + 0.5207
R² = 2E-06
PREFERENCE GREEN CONTROL AVERAGE
y = -0.0009x + 0.4768
R² = 0.015
PREFERENCE AQUA (EGGS ON AQUA/TOTAL EGGS)
GENERATION

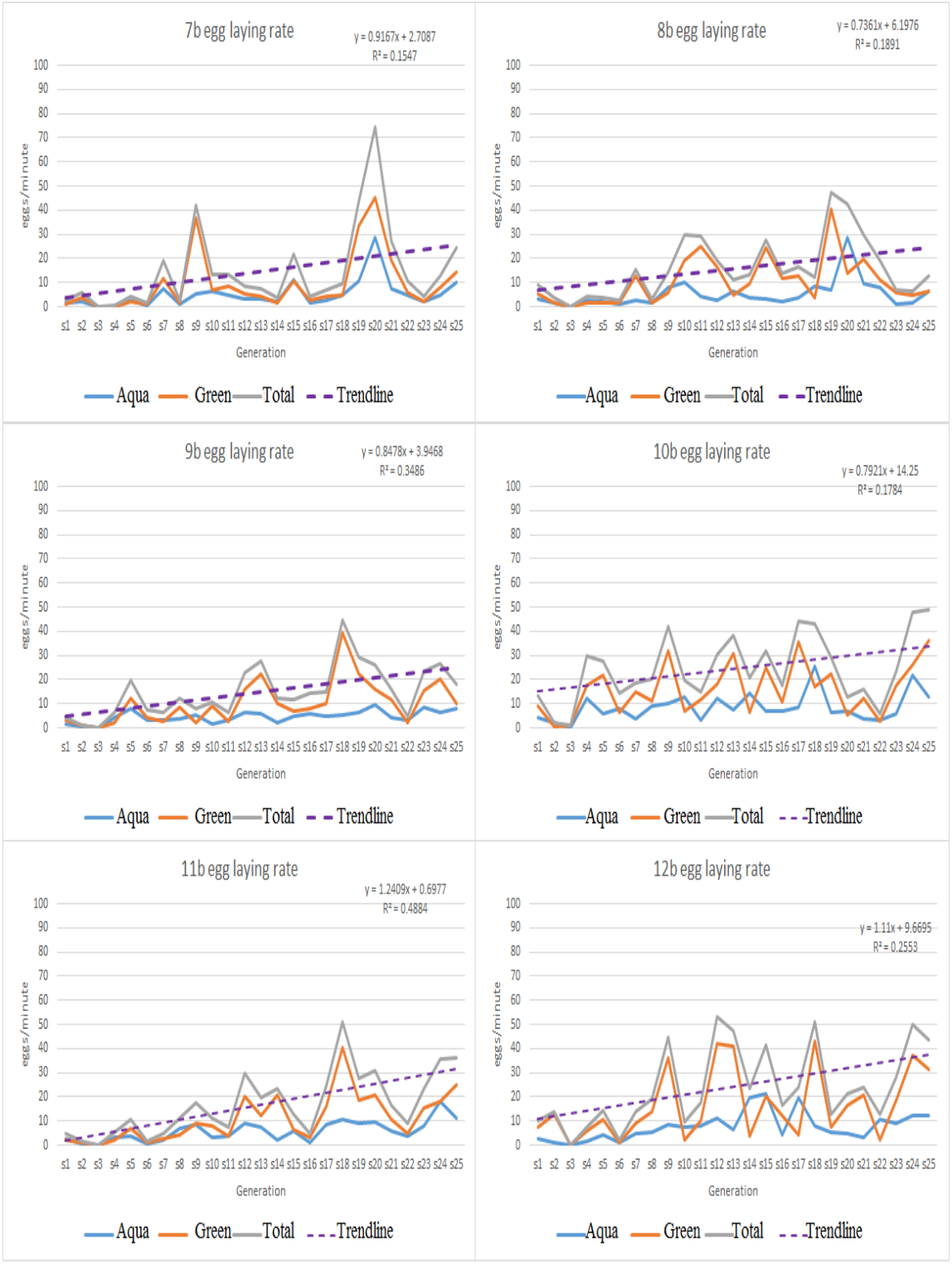

B Lines Preference for Aqua Hue When Every Five Generations Are Averaged Together for Each Replicate
Color Controls Preference for Aqua Hue When Every Five Generations Are Averaged Together for Each Replicate
A Lines Preference for Aqua Hue When Every Five Generations Are Averaged Together for Each Replicate
C Lines Preference for Aqua Hue When Every Five Generations Are Averaged Together for Each Replicate
Aqua Preference (Eggs laid on Aqua)/(Total Eggs)
Averaged Generation
Averaged Generations
gen 1-5
gen 6-10
gen 11-15
gen 16-20
gen 21-25
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

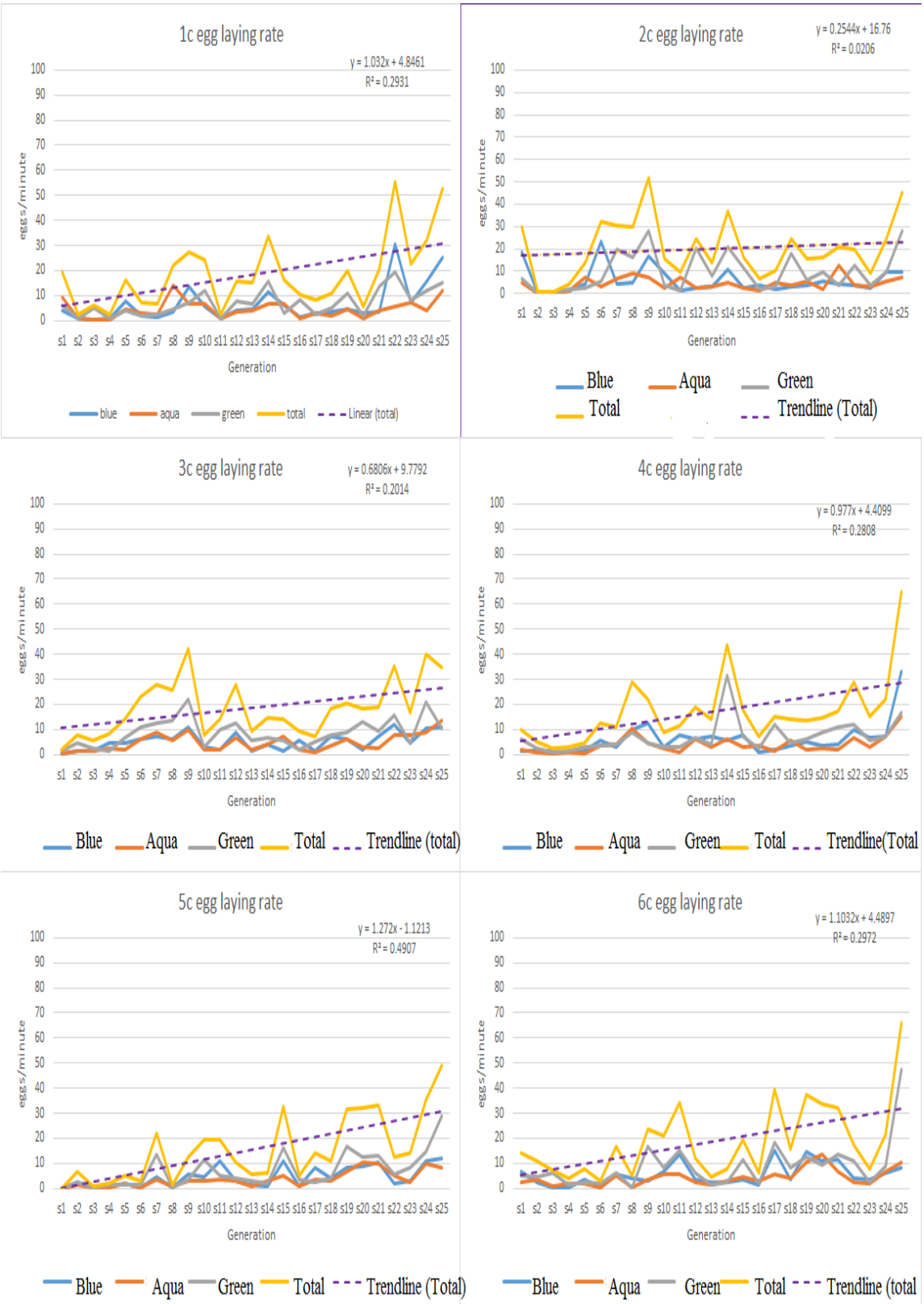
Appendix 5: Egg Laying Rate Graphs

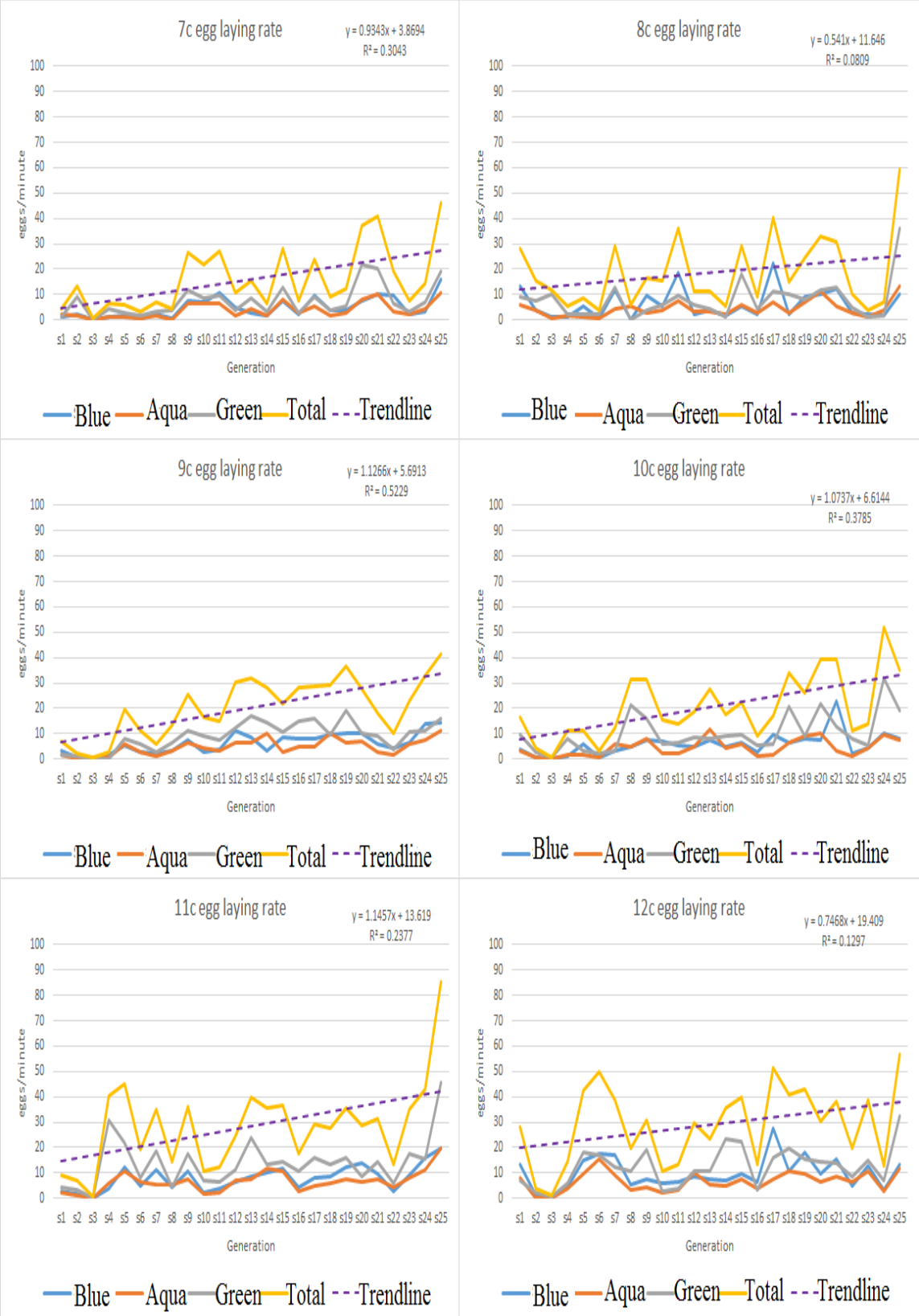


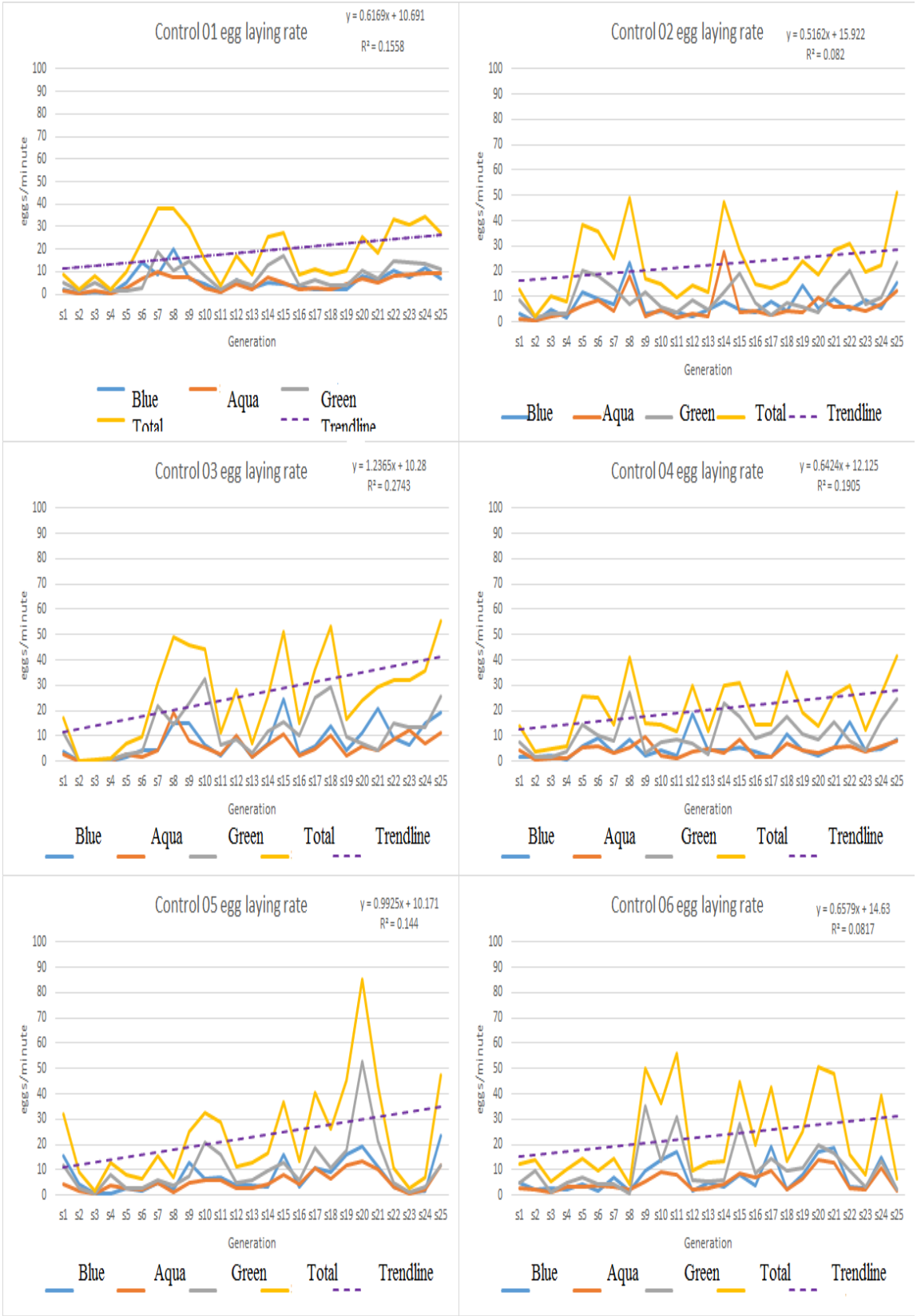

7a egg laying rate
y = 0.5743x + 9.4393
R² = 0.0875
eggs/minute
Generation
Blue
Aqua
Total
Linear (Total)
8a egg laying rate
y = 0.7903x + 7.2115
R² = 0.1521
eggs/minute
Generation
Blue
Aqua
Total
Trendline
9a egg laying rate
y = 0.9529x + 6.7882
R² = 0.2715
eggs/minute
Generation
Blue
Aqua
Total
Trendline
10a egg laying rate
y = 1.099x + 13.637
R² = 0.2355
eggs/minute
Generation
Blue
Aqua
Total
Trendline
11a egg laying rate
y = 1.3202x + 5.8254
R² = 0.3166
eggs/minute
Generation
Blue
Aqua
Total
Trendline
12a egg laying rate
y = 1.4382x + 9.092
R² = 0.3385
eggs/minute
Generation
Blue
Aqua
Total
Trendline

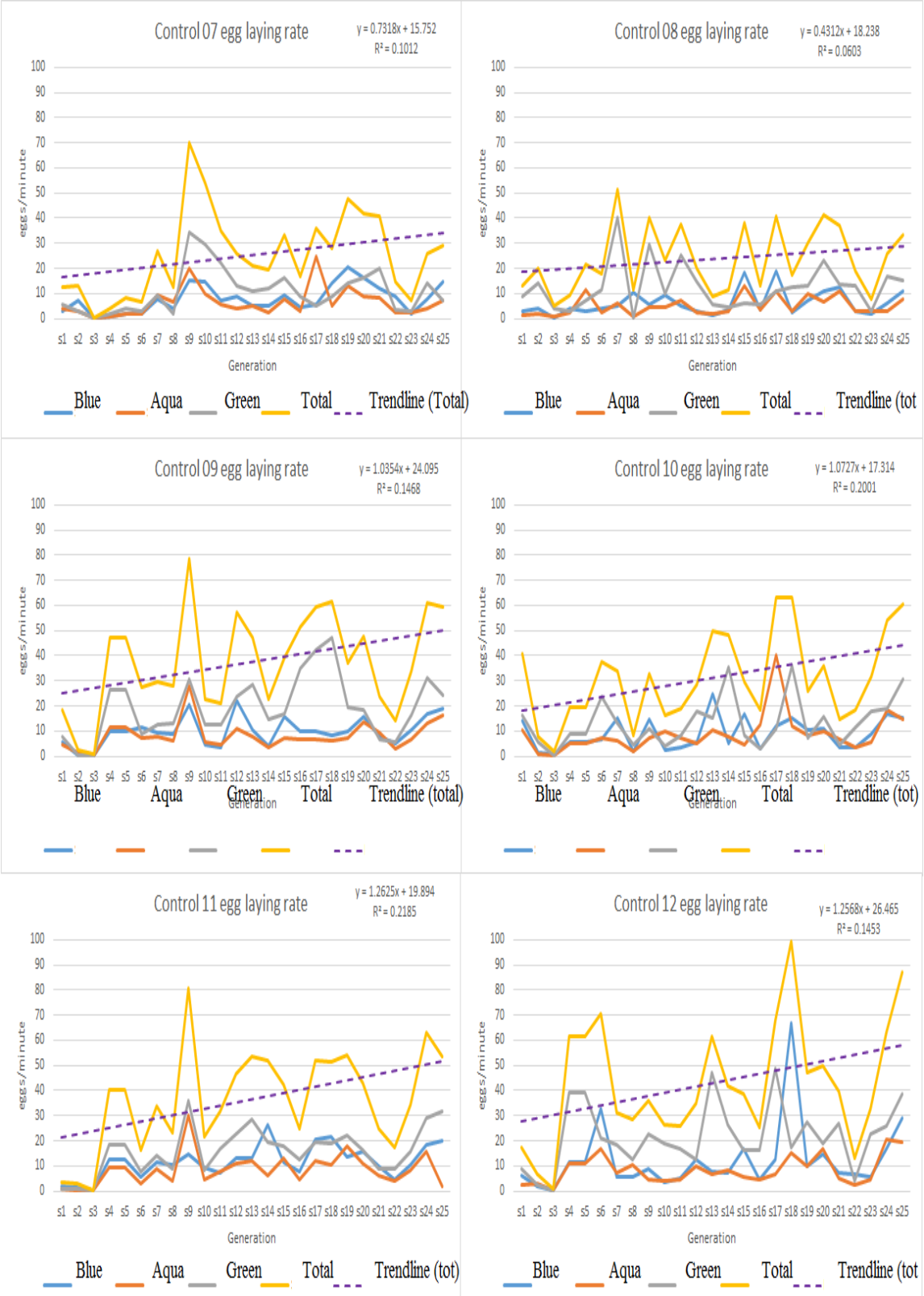

1b egg laying rate
y = 1.4185x - 1.3471
R² = 0.4841
eggs/minute
Generation
aqua
green
total
Linear (total)
2b egg laying rate
y = 1.0128x + 4.2632
R² = 0.326
eggs/minute
Generation
Aqua
Green
Total
Trendline
3b egg laying rate
y = 0.7953x + 6.2287
R² = 0.3277
eggs/minute
Generation
Aqua
Green
Total
Trendline
4b egg laying rate
y = 1.2536x - 0.6528
R² = 0.6608
eggs/minute
Generation
Aqua
Green
Total
Trendline
5b egg laying rate
y = 1.0351x + 0.6833
R² = 0.3539
eggs/minute
Generation
Aqua
Green
Total
Trendline
6b egg laying rate
y = 0.9832x + 1.5119
R² = 0.3266
eggs/minute
Generation
Aqua
Green
Total
Trendline

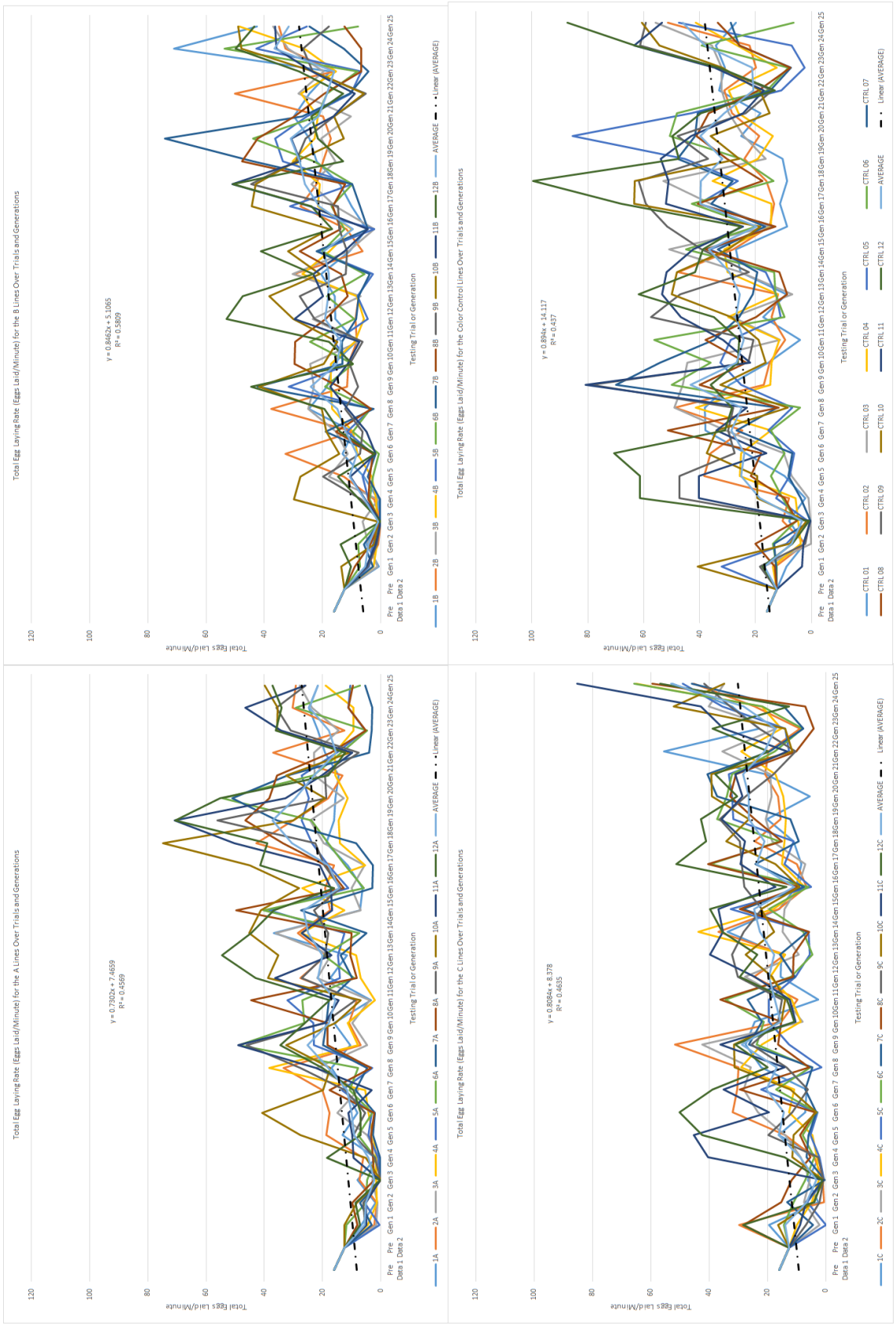

7b egg laying rate
y = 0.9167x + 2.7087
R² = 0.1547
8b egg laying rate
y = 0.7361x + 6.1976
R² = 0.1891
9b egg laying rate
y = 0.8478x + 3.9468
R² = 0.3486
10b egg laying rate
y = 0.7921x + 14.25
R² = 0.1784
11b egg laying rate
y = 1.2409x + 0.6977
R² = 0.4884
12b egg laying rate
y = 1.11x + 9.6695
R² = 0.2553
eggs/minute
Generation
Aqua
Green
Total
Trendline


1c egg laying rate
y = 1.032x + 4.8461
R² = 0.2931
eggs/minute
Generation
blue
aqua
green
total
Linear (total)
2c egg laying rate
y = 0.2544x + 16.76
R² = 0.0206
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (Total)
3c egg laying rate
y = 0.6806x + 9.7792
R² = 0.2014
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (total)
4c egg laying rate
y = 0.977x + 4.4099
R² = 0.2808
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline(Total
5c egg laying rate
y = 1.272x - 1.1213
R² = 0.4907
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (Total)
6c egg laying rate
y = 1.1032x + 4.4897
R² = 0.2972
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (total


7c egg laying rate
y = 0.9343x + 3.8694
R² = 0.3043
8c egg laying rate
y = 0.541x + 11.646
R² = 0.0809
9c egg laying rate
y = 1.1266x + 5.6913
R² = 0.5229
10c egg laying rate
y = 1.0737x + 6.6144
R² = 0.3785
11c egg laying rate
y = 1.1457x + 13.619
R² = 0.2377
12c egg laying rate
y = 0.7468x + 19.409
R² = 0.1297
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline


Control 01 egg laying rate
y = 0.6169x + 10.691
R² = 0.1558
Control 02 egg laying rate
y = 0.5162x + 15.922
R² = 0.082
Control 03 egg laying rate
y = 1.2365x + 10.28
R² = 0.2743
Control 04 egg laying rate
y = 0.6424x + 12.125
R² = 0.1905
Control 05 egg laying rate
y = 0.9925x + 10.171
R² = 0.144
Control 06 egg laying rate
y = 0.6579x + 14.63
R² = 0.0817
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline


Control 07 egg laying rate
y = 0.7318x + 15.752
R² = 0.1012
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (Total)
Control 08 egg laying rate
y = 0.4312x + 18.238
R² = 0.0603
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (tot
Control 09 egg laying rate
y = 1.0354x + 24.095
R² = 0.1468
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (total)
Control 10 egg laying rate
y = 1.0727x + 17.314
R² = 0.2001
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (tot)
Control 11 egg laying rate
y = 1.2625x + 19.894
R² = 0.2185
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (tot)
Control 12 egg laying rate
y = 1.2568x + 26.465
R² = 0.1453
eggs/minute
Generation
Blue
Aqua
Green
Total
Trendline (tot


Total Egg Laying Rate (Eggs Laid/Minute) for the B Lines Over Trials and Generations
y = 0.8462x + 5.1065
R² = 0.5869
Total Eggs Laid/Minute
Testing Trial or Generation
Pre Pre Gen 1 Gen 2 Gen 3 Gen 4 Gen 5 Gen 6 Gen 7 Gen 8 Gen 9 Gen 10 Gen 11 Gen 12 Gen 13 Gen 14 Gen 15 Gen 16 Gen 17 Gen 18 Gen 19 Gen 20 Gen 21 Gen 22 Gen 23 Gen 24 Gen 25
Data 1 Data 2
1B 2B 3B 4B 5B 6B 7B 8B 9B 10B 11B 12B AVERAGE Linear (AVERAGE)
Total Egg Laying Rate (Eggs Laid/Minute) for the Color Control Lines Over Trials and Generations
y = 0.894x + 14.117
R² = 0.437
CTRL 01 CTRL 02 CTRL 03 CTRL 04 CTRL 05 CTRL 06 CTRL 07 CTRL 08 CTRL 09 CTRL 10 CTRL 11 CTRL 12 AVERAGE Linear (AVERAGE)
Total Egg Laying Rate (Eggs Laid/Minute) for the A Lines Over Trials and Generations
y = 0.7302x + 7.4659
R² = 0.4569
1A 2A 3A 4A 5A 6A 7A 8A 9A 10A 11A 12A AVERAGE Linear (AVERAGE)
Total Egg Laying Rate (Eggs Laid/Minute) for the C Lines Over Trials and Generations
y = 0.8084x + 8.378
R² = 0.4655
1C 2C 3C 4C 5C 6C 7C 8C 9C 10C 11C 12C AVERAGE Linear (AVERAGE)

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