

IMPLICATIONS OF INTRASPECIFIC BEHAVIORAL INTERACTIONS ON THE EVOLUTION  
OF THE MBUNA CICHLIDS OF LAKE MALAWI AND THE EFFECTS OF A SMALL CLASS  
INTERVENTION ON A GROUP OF AT-RISK UNDERGRADUATE STUDENTS

by

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## ABSTRACT OF THE DISSERTATION

Implications of Intraspecific Behavioral Interactions on the Evolution of the *Mbuna*  
Cichlids of Lake Malawi and the Effects of a Small Class Intervention on a Group of  
At-Risk Undergraduate Students

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The rock-dwelling cichlids of Lake Malawi, the *mbuna*, are a model system of rapid, sympatric diversification of vertebrates. Though sexual selection has often been invoked to explain their radiation, the best evidence to date suggests that female choice and male-male interactions act to reinforce incipient, allopatric divergence upon secondary contact. First, I expand on the evidence previously gathered on male-male interactions at the inter-population level, by examining within-population behavioral patterns that could explain the diversification of this lineage. Specifically, I measure female preference for conspecific males who are in social isolation and those who are in groups of interacting males. I found that females show preference for males who score higher in male-male contests. In chapter two, I

measure the effect of these male-male interactions on female choice and show that these interactions do affect female preference. By controlling the outcome of each male-male interaction, I show that female preference is affected by the male-male contests themselves. In chapter three, I measure the reflectance of brightly colored, territorial males and look for a correlation between color-similarity and level of aggression between two males. Males show more aggression towards similarly colored conspecific rivals than they do towards rivals who are more differently colored. In chapter four, I measure male reproductive success and the chromatic, behavioral, and territorial traits that affect it. Male color does predict reproductive success. Given my desire to integrate scholarship into every aspect of my academic career, I undertake an investigation on students who are at risk for leaving college because of low academic performance. I describe the social and psychological issues affecting the high rate of college attrition and the effects of a small scale class intervention on student retention, GPA, locus of control, and academic self-efficacy.

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## TABLE OF CONTENTS

ABSTRACT .....	ii
ACKNOWLEDGEMENTS.....	iv
LIST OF TABLES .....	vi
LIST OF FIGURES .....	vii
INTRODUCTION .....	1
SECTION I	
CHAPTER 1: FEMALE MATE PREFERENCE IN THE CONTEXT OF MALE-MALE INTERACTIONS IN <i>MAYLANDIA ZEBRA</i> OF LAKE MALAWI. ....	9
CHAPTER 2: FEMALE <i>MAYLANDIA ZEBRA</i> PREFER VICTORIOUS MALES.....	29
CHAPTER 3: WITHIN POPULATION COLOR-MEDITATED MALE-MALE INTERACTIONS IN <i>MAYLANDIA ZEBRA</i> (FAMILY <i>CICHLIDAE</i> ) .....	44
CHAPTER 4: REPRODUCTIVE SUCCESS ON A SIMULATED LEK ENVIRONMENT .....	69
SECTION II	
CHAPTER 5: TROUBLED TRANSITIONS IN COLLEGE; A STUDY OF THE CAUSES OF ATTRITION AND THE EFFECTS OF A SMALL CLASS INTERVENTION .....	86
ACKNOWLEDGEMENT OF PREVIOUS PUBLICATIONS .....	129
LITERATURE CITED .....	130
CURRICULUM VITAE .....	145

## **LIST OF TABLES**

### Chapter 1:

Table 1.1. Standard length, dominance rank and female preference of males.....21

Table 1.2. Results of Spearman Rank Correlation.....22

### Chapter 3:

Table 3.1. ANOVA table.....58

## LIST of Figures

### Introduction:

Figure 1, Dendrogram of Mbuna Cichlids. ....	4
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### Chapter 1.

Figure 1.1, Cave configuration for male-male aggression measures .....	23
Figure 1.2, Tank design.....	24
Figure 1.3, Spearman rank correlation between male dominance rank and female preference.....	25
Figure 1.4, Spearman rank correlation between male standard length and female preference.....	26

### Chapter 2

Figure 2.1, Tank design.....	39
Figure 2.2, Female preference for each male role. ....	40
Figure 2.3, Effect of assigned role on male attractiveness.....	41

### Chapter 3

Figure 3.1, Location of reflectance measurements.....	59
Figure 3.2, Tank design.....	60
Figure 3.3, Reflectance measurements of study males.....	61
Figure 3.4, Component weightings of each principal component from color data.....	62
Figure 3.5, Plot of individuals according to principal components.....	63
Figure 3.6, Box plots showing male-male aggression.....	64
Figure 3.7, Regression between color similarity and aggression.....	65

## Chapter 4

Figure 4.1, Lek diagram.....	78
Figure 4.2, PCA weightings from color measurements.....	79
Figure 4.3, Reproductive success of males on lek.....	80
Figure 4.4, Proportion of RS of each male.....	81
Figure 4.5, RS, Territoriality and dominance rank of each male.....	82
Figure 4.6, Male PC plots based on color and reproductive success.....	83

## Chapter 5

Figure 5.1, GPA of student categorized by MAP-Works score.....	109
Figure 5.2, Locus of Control, all groups.....	110
Figure 5.3, Locus of Control: low GOA versus higher GPA.....	111
Figure 5.4, Academic self efficacy, all groups.....	112
Figure 5.5, Academic self efficacy low GOA versus higher GPA.....	113
Figure 5.6, Effect of PASS on retention.....	114
Figure 5.7, Effect of PASS on retention.....	115



## INTRODUCTION

The process by which one species divides into more than one, Darwin's "mystery of mysteries" (1845, p. 377) is a principal focus of the natural sciences. The emergence of pre and post-zygotic barriers in allopatric populations that create solid barriers to gene flow upon secondary contact is perhaps the most clear and, probably, the most frequent mechanism by which species multiply (Coyne & Orr, 2004). Barriers to gene flow developing in sympatry, however, is likely much less frequent. Indeed, the point at which one species becomes two during sympatric speciation is almost arbitrary and depends on the species concept most appropriate to the situation and species (Coyne & Orr, 2004). I will define sympatric speciation as a process that is primarily within a single population and lacking any spatial disconnect between incipient species, as discussed in Butlin *et al.* (2008) and Gavrilets (2000).

### *Haplochromine Cichlids as a Model System of Diversification*

Because of their extreme rate of diversification, the haplochromine cichlid fishes of Lake Malawi in southeastern Africa are a model system for the study of speciation (Genner & Turner, 2005). Comprised of 400-600 species (Genner *et al.*, 2004), the haplochromine cichlids have radiated into a wide range of ecological niches over the past 700,000 years (Danley & Kocher, 2001). A primary cause of their unequalled trophic diversity is the relative plasticity of the haplochromine jaw structure over evolutionary time, which has allowed species to exploit a wide range of niches (Hulsey *et al.*, 2010). Two basic jaw structures have developed, which allow for specialization in either suction feeding for those fishes who feed on mobile

prey, such as plankton, or shorter, more stout jaws specialized for foraging on attached prey items, such as snails or algae (Kassam *et al.*, 2004; Albertson & Kocher, 2006). More recently, evolution has resulted in extreme niche specialization, to the point where recently separated populations acquire differences in tooth and jaw shape over a few decades (Streelman *et al.*, 2007).

Not only have the haplochromine cichlids of Lake Malawi radiated into an impressively wide range of niches, more typically occupied by a much broader range of organisms than a single family, but they have also diversified explosively within genera and species through sexual selection (Deutsch, 1997; Danley & Kocher, 2001), presumably by some combination of divergent female choice for male breeding colors (Deutsch, 1997) and disruptive selection caused by color-mediated male-male interactions (Seehausen & Schluter, 2004; Pauers *et al.*, 2008).

The *zebra* species complex is comprised of closely-related members of the *Metriaclima* (*Maylandia*) genus or subgenus, formerly grouped with the *Pseudotropheus* (Konings, 2001; Konings & Stauffer, 2006). Note that the current status of the lineage as either *Metriaclima* or *Maylandia* is in debate (Konings & Stauffer, 2006), a testament to the speed at which these populations evolve and the challenging nature of classifying them. For the purpose of this dissertation, I will generally use *Maylandia*.

The *zebra* species complex is widely dispersed throughout Lake Malawi and thought to have spread throughout the lake approximately 70,000 years ago, as the lake level rose (Genner *et al.*, 2010). Genetic evidence suggests that most populations have remained largely isolated since this most recent expansion

(Genner *et al.*, 2010), though the mechanism by which population divergence occurs remains unclear.

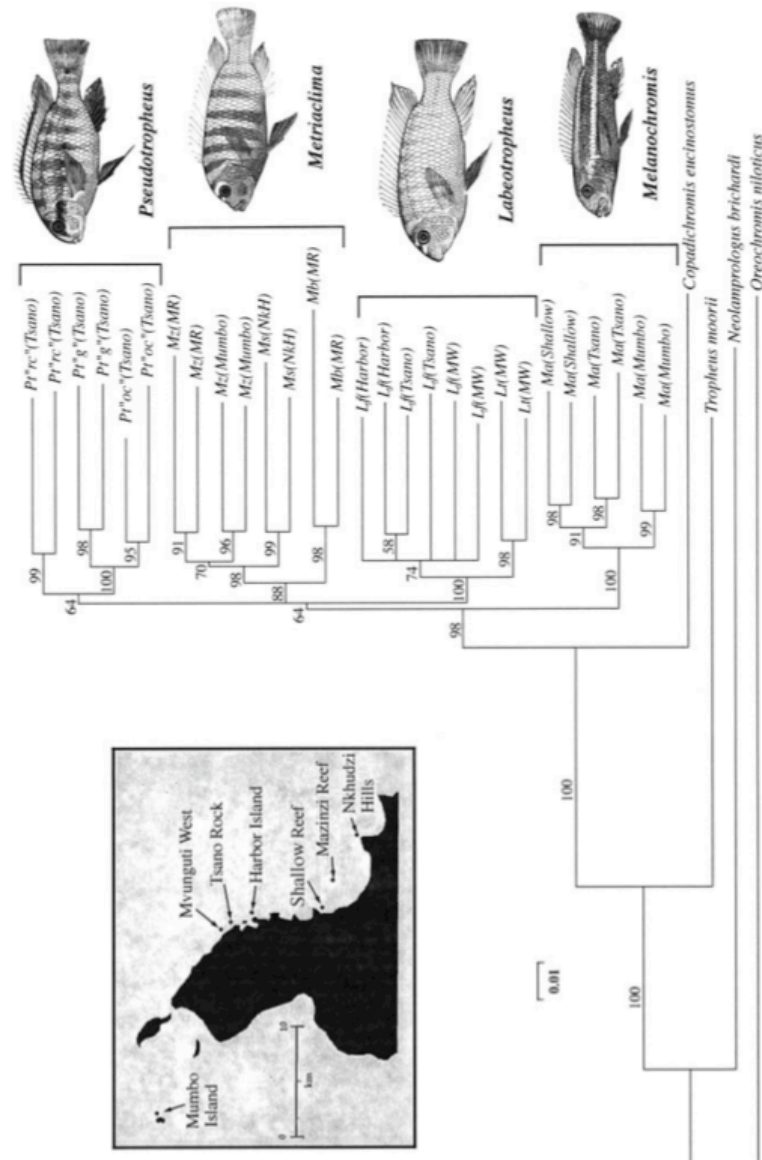


Figure 1: A dendrogram describing the relationships among select Lake Malawi cichlids. This neighbor joining tree is built based on similarity of AFLP banding profiles. Numbers indicate the bootstrap value (percent of trials in which a particular clade was found out of 1000 trials). *Metriaclima zebra* are indicated with the abbreviation “Mz.” Note: *Metriaclima* was recently removed from the genus *Pseudotropheus*, as supported by this analysis. From Allender (2003).

*Evidence for sexual selection affecting diversification: Patterns and Processes*

Though truly sympatric speciation caused by sexual selection is theoretically possible (Higashi *et al.*, 1999), it has not yet been demonstrated. Indeed, sympatric speciation by any mechanism is rare, and among all cichlids has only been conclusively demonstrated in two instances, both small crater lake populations (Schliewen & Klee, 2004; Barluenga *et al.*, 2006). So far, the evidence suggests that sexual selection, operating through both female mate choice and male-male competition, can reinforce nascent differences that develop in allopatry, though there is no evidence that within-population processes can instigate the initial divergence in male breeding colors. Regarding female mate choice, females are known to prefer males from within their own populations to those from neighboring populations (Coultridge & Alexander, 2002; Knight & Turner, 2004). Furthermore, females are known to prefer phenotypically similar males over more closely related males (Jordan, 2008a; Stelkens & Seehausen, 2009). Regarding male-male competition, similar behavioral patterns emerge, where males regard similarly colored rivals as a greater potential threat than more closely related potential rivals that are more differently colored (Pauers *et al.*, 2008).

Courtship and mating occur among the established territories of males inhabiting the near-shore, rocky outcroppings on the lake bottom (Fryer & Iles, 1972). Males establish and maintain territories that are approximately 0.25 m<sup>2</sup> among close-to-shore rocky outcroppings and defend them vigorously from intruders of any species and sex (Holzberg, 1978). Holzberg was also the first to note that reproductive isolation was being maintained through differentiation in

male nuptial colors and could not be predicted through morphological differentiation. These species boundaries were later confirmed through genetic analysis (McKaye *et al.*, 1984).

Between-population and between-genera mate choice (Stelkens & Seehausen, 2009) and male-male aggression studies (Dijkstra *et al.*, 2007b; Pauers *et al.*, 2008) have been conducted that investigate the role of these processes on recently diverged, allopatric populations, and Pauers (2010) suggests that such experiments should continue in order to refine the status of alleged species.

### **Justification for each chapter**

*Chapter 1: Female mate preference in the context of male-male interactions in Maylandia zebra of Lake Malawi.*

The experiments in chapter one are necessary, because models of sympatric speciation by sexual selection require females to discriminate between potential conspecific mates, which has rarely been demonstrated in this group of fishes. I first measure male dominance hierarchies in a novel behavioral test. I then establish that females can distinguish between conspecific males. In addition, I demonstrate that there is a correlation between female preference, male dominance ranking and male standard length. Finally, I show that male-male interactions may be able to affect female preference.

*Chapter 2: Female Maylandia zebra prefer victorious males.*

This study, previously published in the Journal of Fish Biology, demonstrates that it is indeed male-male interactions that affect female preference, and not some

other factor known to correlate with predictors of male contest victories, such as standard length. This is accomplished through a novel manipulation of male behavior by selectively moving males between territories, while in sight of observing females.

*Chapter 3: Within population color-mediated male-male interactions in Maylandia zebra (Family Cichlidae)*

In chapter three, I measure the degree to which males are sensitive to within population color variation. Previous interspecific trials suggest that aggressive bias towards similarly colored rivals could provide the selective pressures necessary to reinforce nascent species boundaries, which evolved in allopatry. This study, however, shows that individual males are sensitive to the color variation within a single population and will direct more aggression towards similarly colored conspecific rivals. This suggests that behavioral interactions could provide the necessary selective forces to incite sympatric speciation.

*Chapter 4: Reproductive Success on a Simulated Lek Environment*

In chapter four, I show that males do not require established territories in order to obtain reproductive success, despite previous suggestions that they do. Furthermore, reproductively successful males appear more red than less successful ones.

*Chapter 5: Troubled Transitions into College and The Effects of a Small Intervention Class*

In chapter 5, I depart from my investigation of the behavioral ecology of cichlid fishes and undertake a study on the causes of student academic troubles and the effects of a small class intervention on cognitive and academic factors. I do this for two reasons. First, I believe that a scholar needs to use the same level of rigor in every aspect of his professional endeavors as is traditionally expected in his research a publications. Second, I desire to utilize a variety of levels of evidence in my scholarly pursuits; studies in human behavior allow for an increased scrutiny of cognitive processes that are impossible to observe in non-human animals. The preliminary investigation that informed the formation of the course revealed only a few institutional variables affecting causes of student attrition. The course was able to affect student retention and academic self efficacy, though it did not have a measurable effect on student GPA.



## SECTION I

### CHAPTER 1

#### **Female mate preference in the context of male-male interactions in *Maylandia zebra* of Lake Malawi.**

Keywords: Mbuna cichlids, sexual selection, male-male competition, female mate choice

#### **Abstract**

The *mbuna* cichlids of Lake Malawi are a diverse, monophyletic and recently derived clade. Sexual selection is thought to have accelerated their rapid diversification, though the mechanism by which this has occurred remains unknown. In this study, we examine the effect that male-male interactions have on female preference. We first used a short interaction experiment as a proxy for male dominance. We then measured female preference for a single, isolated male; a group of three, highly ranked males, relative to a group of lower ranked males; and one mixed group of three mixed-ranked males against a similar group of three mixed-rank males. We found that male dominance was highly correlated with male standard length. Female preference for male standard length and for dominance rank was significant in both isolated and group interactions. However, the coefficient of correlation was larger between female preference and both male

standard length and male dominance rank when females observed groups of interacting males, rather than a single, isolated male. The results suggest that male-male contests influence female mating decisions. By elucidating the rules that dictate the outcomes of such interactions we can elucidate the role that behavior plays in the diversification of this species-rich lineage.

## Introduction

The haplochromine cichlid fishes of Lake Malawi represent one of the most rapidly speciating groups of vertebrates (Seehausen, 2000). Danley and Kocher (2001) described the diversification of these fishes as a three-stage radiation through natural selection and at a finer scale, sexual selection. Mechanisms related to male-male interaction and to female choice of male breeding color patterns have been used to explain the diversity of morphologically similar forms (Coultridge & Alexander, 2002; Seehausen & Schluter, 2004).

Among the 450-600 haplochromine cichlids found in Lake Malawi, the *mbuna* represent about 295 species (Konings, 2001; Genner *et al.*, 2004). Brightly colored members of a monophyletic group, the *mbuna* inhabit rocky outcroppings within the lake. All *mbuna* are maternal mouthbrooders that lack a larval dispersal stage and exhibit a high degree of philopatry. The rocky habitat serves as a lek-like arena, within which male *mbuna* establish and defend territories and actively court visiting females. Females do not hold territories and are known to visit multiple males (Fryer & Iles, 1972).

The sexual dichromatism, disparity in parental care, and the diversity in male breeding colors have led researchers to focus on the role of female mate choice on the reproductive success of males and on the evolution of the system. Previous work has focused on female choice for color patterns in heterospecific tests and has found that females prefer conspecific males over heterospecific males (Coultridge & Alexander, 2002; Jordan *et al.*, 2003) as well as similarly-colored heterospecific males over differently colored heterospecific males (Coultridge & Alexander, 2002; Jordan *et al.*, 2003). However, it has proven to be much more difficult to demonstrate female preference for one conspecific male over another, or to find a trait that females use to discriminate between conspecific males, especially in dichotomous choice tests where only a limited amount of information is available for females to assess male quality. Recent work shows that an absence of chromatic information does not seem to affect assortative mating, suggesting that other cues (perhaps behavioral or olfactory) are used by females in making mate choice decisions (Blais *et al.*, 2009).

Recent studies, however, have suggested that male body coloration might be more than just a signal intended for females. Male nuptial colors may also be a signal used between males (Jordan *et al.*, 2004; Seehausen & Schluter, 2004; Pauers *et al.*, 2008; Jordan *et al.*, 2010). Pauers *et al.* (2008) found that males show higher levels of aggression toward similarly colored heterospecifics than towards the phylogenetically more closely-related, but differently colored, heterospecific males. Males showed similar levels of aggression to similarly colored heterospecific males as they did toward conspecific male rivals. Likewise, females use gross color pattern,

instead of phylogenetic relatedness, to assess potential mates (Couldridge & Alexander, 2002; Jordan, 2008a). Taken together, these data suggest that female mate choice and male-male competition may interact in a synergistic manner to determine ultimate mating success. Further examination of the factors influencing female mate choice, other than male body coloration *per se*, seems warranted.

In addition, these interspecific experiments do not investigate the mechanisms that affect the relative mating success between conspecific males. It is possible that the mechanisms that are responsible for the rapid diversification of this lineage occur within populations, i.e., that disruptive selection is causing sympatric speciation. In order to determine the likelihood of diversification by sympatric versus allopatric mechanisms, we must understand the traits that affect reproductive success within populations.

It is known that conspecific males of many *mbuna* species will interact aggressively with one another, resulting in dominance hierarchies (Andries & Nelissen, 1990), thus providing a potentially rich set of information for females to assess potential mates. Given the difficulty in finding strong variation in female preference for one male trait over another, in the absence of behavioral cues, this study focuses on the role of conspecific male-male competition on female choice. In this study, we investigate the potential for male-male aggressive behavior to be a cue that females use to select mates. Theory suggests that females should use male dominance ranking in their mate choice decisions (Qvarnstrom & Forsgren, 1998). The presumption is that dominant males are able to provide females greater direct or indirect benefits. There is no evidence that males offer direct benefits to females

in this system, so we suspect that if females demonstrate preference for male behavior, it will be for the indirect benefits offered, such as those derived from “good [paternal] genes” for the progeny (Andersson, 1994).

Specifically, we test the hypothesis that females will preferentially associate with males that succeed in aggressive interactions. A positive correlation between male dominance rank and female preference could suggest that traits that affect male interactions also affect female preference, though additional investigation would be warranted. We also test the hypothesis that female preference is stronger when observing two groups of interacting males that differ in dominance rank than when observing groups of males that do not differ in dominance rank. If females discriminate between groups of dominant versus sub-dominant males, but fail to discriminate between mixed groups of males, then it would suggest that females also use additional behavioral cues in their specific mate choice decisions.

## **Methods**

Experimental fish were sexually mature, laboratory-reared *Maylandia zebra* (Boulenger) F1 and F2 descendents of wild caught individuals from the Mazini Reef area of Lake Malawi (approximately 14° 05' S, 34° 56' E). Sexual maturity was determined by male adoption of bright coloration and is typically reached when an individual grows to about 80 mm standard length (personal observation), though a few of the experimental fish were shorter than this but still deemed to have reached sexual maturity based on coloration and territorial behavior. Fish were housed in

individual, 19 L tanks for at least two months prior to use in the experiment, on a 12 hour light-dark cycle under broad spectrum lighting and fed once per day.

*Maylandia zebra* are an ideal model species for the whole *mbuna* group because they exhibit traits characteristic of the entire lineage, are sexual dichromatic, practice maternal mouth brooding, followed by maternal care, and they are common and widespread throughout Lake Malawi.

### *Experiment 1*

First, male dominance hierarchies were established and measured. To do this, twenty males of similar size were selected and randomly assigned to either Group A or B, each consisting of ten fish. All ten males from one of the two groups were placed simultaneously into a 56 litre tank, containing a group of rocks arranged to form a single cave-type territory (figure 1.1). Males are known to prefer rocky, cave-like territories, the value of which is apparent, given the fact that female preference for high quality territories may take precedence over other factors (Dijkstra *et al.*, 2007a). The individual male that adopted bright coloration and successfully chased other males from the territory was assumed to be dominant and was subsequently removed. The process was repeated until only one fish remained. Dominance was always apparent within three minutes. Three replicates for each group were conducted, with a week between replicates. Each male was then assigned a dominance rank based on the median of the three trials. Spearman's rank correlation tests were used to measure the correlation between male standard body length and median dominance rank. Through trial and error, ten males seemed an ideal grouping to stimulate interaction. Using more than ten fish increased the time

it took for one individual to establish dominance, which increased the possibility of injury to the fish.

### *Experiment 2*

Next, female choice was measured in two experiments to determine the correlation between male dominance and female choice. The combined aim of these two experiments was to tease apart whether male morphological/chromatic traits or male-male behavioral interactions were the basis of female preference. A single stimulus male was used in Experiment 2, and combinations of males were used in a dichotomous choice design in Experiment 3. A combination of single and multi-stimulus designs was chosen because standard dichotomous choice in which a focal female chooses between two males has not yielded consistent results in intra-species choice trials for this group of fishes (Jordan, 2008a).

In Experiment 2, all 20 males from the dominance hierarchy experiment were used as a stimulus. A male and a female were placed into separate compartments of a 56 litre (750 mm x 250 mm x 300 mm) aquarium. Males were confined to 1/3 of the aquarium by a single transparent acrylic partition to prevent injury to the female. Trials were separated by 15 minutes to allow males to rest and they were repeated with 12 females for each male. Behavior was recorded for 10 minutes and the time spent at the partition by the female (association time,  $t_a$ ) was measured. Previous studies have verified the validity of using female behavior prior to contact with the males to predict female mate choice (Kellogg *et al.*, 1995; Couldridge & Alexander, 2001). Males were ranked by their median  $t_a$  across all 12 females. The rankings were used as response variables in Spearman rank

correlation tests. Two comparisons were made for each hierarchy: one using median dominance rank and the other using male body length as the predictive factor. Any ties in rank were assigned the median value. The dominance rankings and the response variables of groups A and B were combined for analysis.

### *Experiment 3*

In the second female choice experiment, two configurations in which males were sorted by dominance ranking were used as stimuli. Twelve females were used and female preference for one of two groups of interacting males was measured. In each configuration, three, nine litre (300 mm x 200 mm x 150 mm) aquaria were grouped at the left and three at the right ends of a 40 litre (630 mm x 320 mm x 200 mm) aquarium that held a female (figure 1.2). The arrangement of aquaria was designed to allow male fish to see and interact with each other, while preventing them from injury. For the first configuration, three of the five most dominant males from Experiment 1 were placed in either the left or right grouping of small tanks and three of the five least dominant males were grouped on the opposite side. The second configuration consisted of a mix of dominant and non-dominant males grouped together on either side of the female's aquarium. Stimuli fish were acclimated for 2 hours. The test female was introduced to the centre of the large tank and acclimated for 15 minutes. After each trial, males were removed and new clusters were assembled, such that males were used more than once, whereas clusters were unique. Dominant and non-dominant clusters were alternately placed on the left and right sides of the arena. This was repeated 12 times using 12 different females. Each trial was video-recorded for 15 minutes and  $t_a$  was



measured from the recordings.  $T_a$  was defined as time spent by the female in either the left or right third of the aquarium. In order to compare the results of this experiment with Experiment 2, a Spearman rank correlation was again used, where the two interacting variables were the mean dominance rank of the group of three males and  $T_a$ . The correlation between mean male body length and female preference ( $T_a$ ) was also measured. Results were also partitioned by side (left or right) to test for female side bias.

## Results

In the male dominance hierarchy experiment, Experiment 1, for group A, two males immediately began contesting the cave territory by brightening their color, extending fins, and 'flashing'. Ramming and biting occurred in trial 2, necessitating the removal of one fish to prevent serious injury. In trial 3, the preferred site shifted from the initially preferred site to another 'cave', although the dominant male also ejected males from the initial site, but with less rigor than the preferred site (table 1.1). The trials for group B proceeded with no removals necessary and no change in preferred territory. The hierarchies for both groups were generally stable over the three trials with minor shifts in rank (table 1.1). Because dominance rank was generally stable between trials, we believe that this is an accurate measure of male aggression (see discussion). In both groups, male standard body length was significantly correlated with median dominance rank (Spearman Rank Correlation; Group A:  $n = 10$ ,  $r_s = -0.91$ ,  $P < 0.01$ ; Group B:  $n = 10$ ,  $r_s = -0.86$ ,  $P < 0.01$ ).

In Experiment 2, males immediately began to court females introduced on the opposite side of the colorless partition. Both male median dominance ranking (Spearman Rank Correlation:  $n = 12$ ,  $r_s = 0.771$ ,  $P = 0.015$ ) (figure 1.3) and male standard body length (Spearman Rank Correlation:  $n = 12$ ,  $r_s = 0.075$ ,  $P = 0.019$ ) (figure 1.4) were significantly correlated with female preference rank (table 1.2).

In trials with groups of highly dominant versus less dominant males in Experiment 3, male interactions typically occurred as soon as males were within visual contact with each other. Males on the same side of the female's central tank typically showed aggressive behaviors towards their neighboring males, such as biting the colorless glass barriers between tanks, swimming in vertical, repeating, linear patterns, while oriented towards their neighbor, and occasional shimmering. Significant correlation was found between male dominance ranking and female preference and between total body length and female preference (table 1.2). However, no such correlation was found when mixed groups of males were used. No side bias was detected in female preference (Wilcoxon,  $n = 24$ ,  $Z = 0.171$ ,  $P = 0.86$ ).

## Discussion

Two conclusions can be drawn from these results. First, females preferentially associate with larger and more dominant males. Second, the correlation between male dominance and female preference is closer to a perfect correlation ( $r_s$  of +1 or -1) when females are able to assess interacting males ( $r_s$  of 0.740) than when females observe males that are not interacting ( $r_s$  of 0.651) (table 2). The second finding implies that females are able to distinguish between males

based on dominance ranking within a group of interacting males, although it is possible that size is the primary trait by which females assess interacting males. This suggests that male behavior on the lek may communicate information necessary for females to discriminate between conspecific males.

These findings imply that male interactions are an important element of a complete framework for understanding the rapid diversification of this group of vertebrates. Jordan *et al.* (2010) and Mellor *et al.* (2010) recently suggested that female *M. zebras* use conspecific male interactions to assess potential mates. Together with the results presented here, it appears that female choice and male-male interactions interact with one another and should be considered together in studies of sexual selection in the *mbuna* cichlids.

We acknowledge that the male dominance measurement in Experiment 1 is not of actual territorial establishment, but the goal of this study is not to mimic territory formation. Rather, the object is to measure gross patterns of male aggressive interactions. We believe that the robustness of this measure combined with the correlations seen between this measurement and the female preference measurements suggest that we are recording real phenomena that are not an artefact of unrealistic, laboratory-based experimental design.

Though it has long been known that sexual selection likely amplifies the rate of diversification, the mechanism for such rapid speciation has only been demonstrated in heterospecific trials. Diverging preference within a population is necessary for sympatric speciation by sexual selection, and our findings suggest that hypothetical color-mediated antagonistic interactions could be the basis for

diverging female preference among conspecific males, as suggested previously in inter-species tests (Seehausen & Schluter, 2004; Pauers *et al.*, 2008).

While past studies of sexual selection in *mbuna* have focused primarily on male-female communication, here we present an indication that male-male interaction deserves greater attention in the study of mate choice for this group. Furthermore, the role of intraspecific interactions has, in our opinion, been underemphasized in recent work, though it is necessary if we are to rule out or find support of sympatric speciation.

Table 1.1: Standard Length, Body Depth, and Dominance Rankings (Experiment 1) of Males, and Means of Association Time/Total Time (Experiments 2). n=12 for each mean as 12 females were used in each group. Females were not reused between groups.

Group	SL (mm)	Depth (mm)	Dominance rank in three trials	Ranked by median dominance score	Mean $t_a/t_t$	Female preference rank
A	90	25	1,2,1	1	0.44	1
A	86	24	2,1,2	2	0.34	3
A	83	22	3,4,3	3.5	0.27	5.5
A	90	24	4,3,3	3.5	0.35	2
A	83	24	5,5,5	5	0.28	4
A	83	23	6,6,6	6	0.12	9.5
A	79	22	7,7,7	7	0.27	5.5
A	79	22	8,8,8	8	0.26	7.5
A	77	20	9,9,9	9	0.26	7.5
A	69	19	10,10,10	10	0.12	9.5
B	92	24	1,1,1	1	0.55	4
B	96	24	2,2,3	2	0.57	3
B	95	24	4,5,2	3	0.61	2
B	100	25	5,3,4	4	0.50	6
B	81	19	6,8,3	5.5	0.44	8
B	86	20	4,6,7	5.5	0.53	5
B	82	19	8,5,7	7	0.42	9
B	85	18	7,6,8	8	0.48	7
B	78	19	9,9,9	9	0.62	1
B	76	18	10,10,10	10	0.38	10

Table 1.2: Results of Spearman's Rank Correlation

Stimulus Correlation	Single male	Groups of three males, segregated by high and low rank in hierarchy	Groups of three males, each group a mix of high and low ranked males
<b>Hierarchy &amp; female preference</b>	$N = 20, r_s = 0.651, P < 0.01$	$N = 12, r_s = 0.740, P < 0.0001$	$N = 12, r_s = 0.016, P = 0.94$
<b>Male total length (mm) &amp; female preference</b>	$N = 20, r_s = -0.585, P < 0.01$	$N = 10, r_s = -0.746, P < 0.0001$	$N = 10, r_s = -0.010, P = 0.96$



Figure 1.1

Cave configuration in which male-male aggression scores were made.

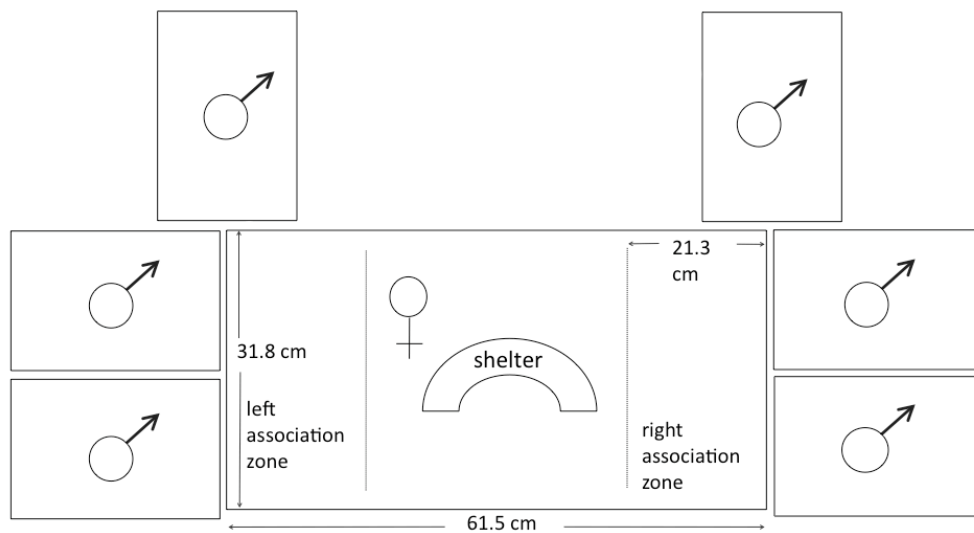


Figure 1.2:

Tank design for experiment 3, in which female association was measured between groups of interacting males. Females were exposed to two scenarios: 1) groups of interacting dominant males versus submissive males or 2) two groups of mixed-rank males.



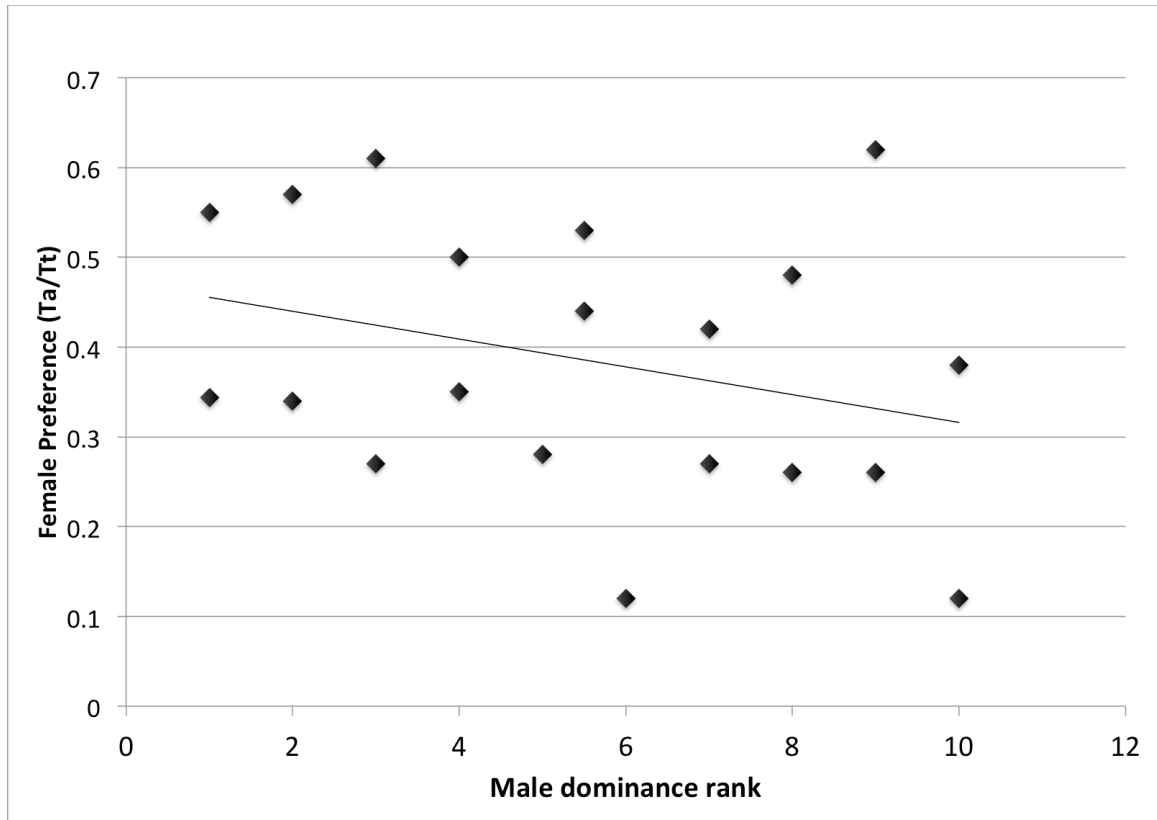


Figure 1.3

More dominant males, i.e., those with a lower dominance score, were more highly preferred by females than less dominant males.

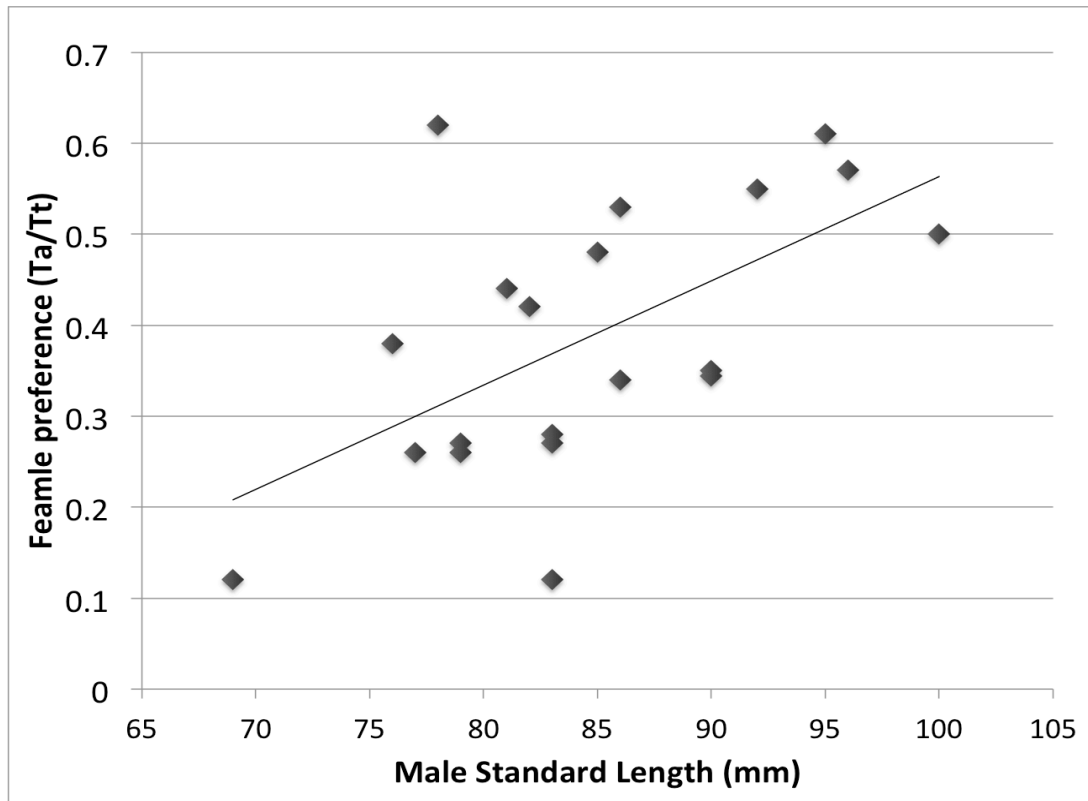


Figure 1.4

Longer males were more preferred by females than shorter males.

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## CHAPTER 2

### **Female *Metriaclima zebra* prefer victorious males.**

Females of a widespread species of the rock-dwelling haplochromine cichlids of Lake Malawi, *Metriaclima zebra*, show preference for males who successfully evict intruding males from their territory. This behavior, experimentally induced by the investigators in a laboratory setting, was also preferred over males that were not permitted to interact with any other individual.

Key words: Male-Male Competition; Behavior; Sexual Selection; Haplochromine cichlids; Mbuna

## Abstract

Aggressive male-male contests are a widespread phenomenon amongst vertebrates and are considered one of the common types of interactions involved in sexual selection (Darwin, 1871; Andersson, 1994). These intrasexual contests are often studied separately from female mate choice even though there are many reasons why female preference should be influenced by male-male competition (Qvarnstrom & Forsgren, 1998). For example, male-male contests may be an honest signal of genetic quality or of an ability to provide direct benefits. The intense male-male competition for territories and opportunities for female choice among the rock-dwelling haplochromine cichlids of Lake Malawi present an unusual opportunity to study the interactions between these two processes.

## Introduction

The haplochromine cichlid fish of Lake Malawi, a model system for studying sexual selection and speciation, represent one of the most diverse and rapidly speciating groups of vertebrates (Danley & Kocher, 2001). The *mbuna*, or rock-dwelling haplochromine cichlids, are a particularly speciose group consisting of approximately 250 species that originated within the past million years (Konings, 2001; Genner *et al.*, 2004). The pattern by which male breeding colours are distributed among the *mbuna* suggest that sexual selection results in keeping similarly coloured species distinct (Allender *et al.*, 2003). The diversification of Lake Malawi *mbuna* has been accelerated by sexual selection in two ways. Some studies

have found evidence that intersexual selection by female mate choice for divergent male colour patterns is primarily responsible for the diversity of male colour patterns (Barlow, 2000; Danley & Kocher, 2001). Others have found evidence that intrasexual selection via male-male interactions can account for the observed patterns of diversity (Seehausen & Schluter, 2004; Pauers *et al.*, 2008).

The *mbuna* occur on rocky outcroppings in lek-like assemblages in which conspicuous males establish, maintain and defend territories (Fryer & Iles, 1972; Ribbink, 1991; Barlow, 1993). These territories are not only the primary sites of courtship and mating, but are also used for feeding and are maintained for as long as the male can defend it from other males (Ribbink, 1991; Barlow, 1993). Females inspect males on their territories and following ritualized courtship they may mate with one or multiple males (Kellogg *et al.*, 1995; Parker & Kornfield, 1996). To explain patterns in reproduction, previous research has found support for the role of female choice on male colouration (Coultridge & Alexander, 2002; Jordan *et al.*, 2003). Based on observations from across the cichlids of Africa's Great Lakes, it is possible that the territories themselves are the objects of female choice (e.g., Malawi bower builders, McKaye *et al.*, 1990; Victoria haplochromines, Dijkstra *et al.*, 2007a; and Tanganika co-operative breeders, Kohda *et al.*, 2009).

Recently, though, it has been suggested that male-male competition could *directly* affect the diversification of male breeding colour patterns, and thus species richness, of this lineage (Seehausen & Schluter, 2004; Pauers *et al.*, 2008). New evidence suggests that males behave more aggressively toward similarly coloured

males than toward males displaying more divergent colour patterns (Pauers *et al.*, 2008). This phenomenon was demonstrated by comparing aggression between similarly coloured heterogeneric males and between differently coloured congeneric males.

This study focuses on the effect that male-male contest competition has on female preference. It is predicted that if females use male-male interactions to make mate choice decisions, then females will discriminate between males by differentially associating with winners of male-male interactions. Below, a study is described where male behavior is manipulated wherein male-male interactions have predetermined outcomes. Males are assigned the role of territorial “winner,” invading “loser,” or “non-interactor” in a territory dispute observed by a female. Female preference for each role is then measured.

## Methods

Experimental fish were second-generation descendants of wild-caught *Maylandia zebra* Boulenger from the Mazini reef area of Lake Malawi (14° 05' S, 34° 56' E). Male breeding colors are all blue with six to eight vertical black bars along the lateral sides. The *M. zebra* species complex within the *mbuna* consists of closely related, diverging populations. Because of their genetic similarity and phenotypic diversity, especially in regard to male breeding color patterns, this likely represents a complex currently diversifying by sexual selection (Danley & Kocher, 2001). Fish were housed in individual tanks for at least two months prior to use in the



experiment on a 12 hour light-dark cycle under broad spectrum lighting and fed once per day. Gravid females ( $N = 9$ ) were used. Experimentation occurred in the laboratory and fish were returned to stock at the completion of the experiment.

Six males were used for the stimuli. This number was sufficient to ensure unique combinations of stimuli during trials, thus avoiding pseudoreplication in that each female always saw a unique combination of males. The role (winner, loser, or non-interactor) and therefore the behavior of the males was artificially manipulated. This controlled for other factors of behavior such as size, previous experience, and inherited traits. Using a small number of males ensured that each male was used for all social ranks, thus ensuring that female preference was measured as a function of behavior and not of any other trait.

The experiment was conducted using a multi-partitioned arena as modified from Grosenick (2007) (figure 2.1). A traditional dichotomous choice design was not used because these eliminate the ability to investigate complex social interactions. Test females occupied the central compartment, from which they could observe four treatment types: 1) a losing male, 2) a non-interacting male, 3) a winning male and 4) a female. While the strongest interest was in comparing the attractiveness between 1 and 3, treatments 2 and 4 were used as controls to ensure that females were not interacting with the winning or losing male as a means to simply interact with any other fish. The only transparent barriers were between the central female and the peripheral chambers being used during a given trial. All partitions between peripheral chambers were opaque. The size of the males' compartments was

reduced by 50% from the full length of the tank to the size indicated in figure 2.1 in order to force males to interact with one another. The size of the female compartment was the full length of the tank, and because the measure of female preference was the time spent interacting with a fish in a given compartment instead of time in proximity to a particular compartment, no correction for compartment size was necessary. Males were allowed to acclimate in their individual territories for two hours prior to introduction of the females. This time was found to be sufficient for males to display territorial behavior, including manipulation of the rocky substrate.

Females were added to their assigned compartments and acclimated for 10 minutes, as has been used in similar studies measuring female preference (Couldridge & Alexander, 2001). One male was then removed from its compartment, suspended in a net out of the water for 30 seconds, and placed in the compartment of one of the other males. The combined stresses from being removed from the water and placed in an unfamiliar territory was a reliable method of assuring that the territory-holding male directed more aggression towards the invader than the other way around. The invading male was returned to its compartment after five minutes, although sooner if there was risk of serious harm because of intense aggression. Females were able to observe the interactions through the transparent acrylic partitions. The arena was then recorded for 10 minutes by a video camera suspended above the arena. All fish were returned to their original tank outside of the testing area following a trial. The procedure was repeated three times for each

female using unique combinations of males. Trials for any female were separated by at least 24 hours.

Female association with each treatment was scored from the video recording as the time the female was within 80mm of a treatment fish and oriented towards that fish. Time spent in proximity to a male is a reliable proxy for eventual mate choice decisions (Couldridge & Alexander, 2001) and the authors believe that including the requirement for females to be oriented towards a fish adds to the reliability of this score. Two raters independently scored 30% of the videos and discussed results until complete agreement was achieved. One rater subsequently scored the remaining videos. Proportion of time spent interacting was calculated by dividing the time spent associating with a particular fish by the total amount of time the female was oriented towards any of the four fish ( $T_a \times T_t^{-1}$ ). Note that this measure includes only time that females spent associating with a treatment. Statistical analysis was completed using a Friedman test to compare the median female preference for each of the four treatments (winner, loser, non-interactor, and extra female) and a second Friedman test to compare the median attractiveness of the males when they were assigned to each of the three roles (winner, loser, and non-interactor). Wilcoxon signed rank tests were used for post hoc comparisons. These nonparametric tests were chosen because of the lack of independence and of normality in the measures of association time.

Females spent on average 91% of their total time associating with one of the treatments (S.D. = 9%). Overall, females spent significantly more time associating with territorial males versus other treatments (Friedman,  $N = 9$ ,  $P < 0.01$ ) (figure 1.2). Post-hoc, pair wise analysis suggests that female preference was identical for each treatment except for territorial males (Territorial versus non-interacting: Wilcoxon,  $N = 9$ ,  $P < 0.05$ ; Territorial versus invader: Wilcoxon,  $N = 9$ ,  $P < 0.05$ ; Territorial versus extra female: Wilcoxon,  $N = 9$ ,  $P < 0.01$ ; Non-interacting versus invader: Wilcoxon,  $N = 9$ ,  $P > 0.05$ ; Extra female versus non-interacting, Wilcoxon:  $N = 9$ ,  $P > 0.05$ ; Extra female versus invader: Wilcoxon,  $N = 9$ ,  $P > 0.05$ ). Likewise, male attractiveness was significantly different between each status treatments (Friedman,  $N = 6$ ,  $P < 0.05$ ) (figure 2.3). Post-hoc, pair wise analysis suggests males were more attractive when successfully holding territories than in either of the other two treatments, which were not significantly different from each other (Territorial versus non-interacting: Wilcoxon,  $N = 6$ ,  $P < 0.05$ ; Territorial versus invader: Wilcoxon,  $N = 6$ ,  $P < 0.05$ ; Invader versus non-interactor: Wilcoxon,  $N = 6$ ,  $P > 0.05$ ).

Smaller sample sizes can raise concerns about statistical power. In the Friedman test, the average difference in median proportion of time spent associating with invading males versus the other treatments was 21%, whereas median differences of either 1% or 7% were found between treatments not found to be statistically significant. The 7% difference found between non-interacting males and invading males could be biologically meaningful and may warrant future study if there is reason to investigate the benefits of unsuccessful contests versus avoiding all contests, though this was not the focus of this investigation. Given these

limitations, sample size was sufficient to detect a statistical significance between invading males and all other treatments.

## Discussion

To the authors' knowledge, these are the first data to support the notion that male-male contest competition can be used by females to make mate choice decisions in this diverse system. Indeed, despite significant efforts, there is very little evidence that females discriminate to any degree between conspecific males during courtship (Pauers *et al.*, 2004). The fact that contests between males can themselves be the object of female choice suggests that these interactions can have a more substantial role in male reproductive success than previously reported (see Barlow 2000, for examples). Furthermore, these results lend support to the idea that male-male interactions could act as a diversifying force in these cichlid fish as posed by Seehausen and Schluter (2004) and supported by Pauers *et al.* (2008). Though there are many possible reasons why females prefer winners of territorial disputes (Qvarnstrom & Forsgren, 1998), the most likely is that females gain indirect benefits, such as so called "good genes," rather than any direct benefits.

These data are not sufficient to fully understand the role of sexual selection in the *mbuna* model system. In order to fully explain their recent diversification, there must be evidence of disruptive selection occurring at the population level in directions that predict the observed diversity. This ephemeral stage in speciation is difficult to observe, as it can quickly lead to directional selection in two new

populations (Pauers *et al.*, 2004). It is theoretically possible that sexual selection can act as a diversifying force in sympatric speciation (Turner & Burrows, 1995), but the idea is controversial (Arnegard & Kondrashov, 2004). Finally, it must be demonstrated that males show more aggression towards similarly colored male rivals that are within the amount of color variation that occurs within a population if one is to assert that diversification in this lineage can be caused by sexual selection.

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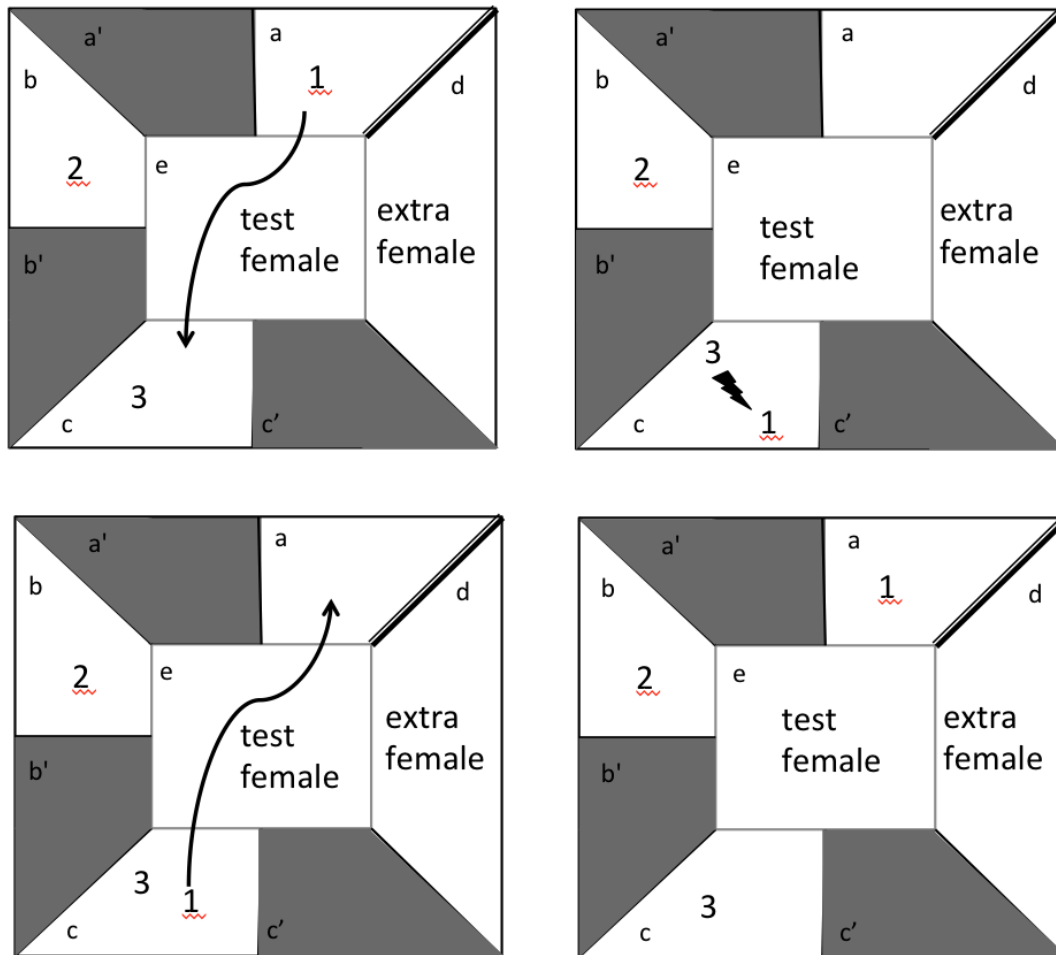


Figure 2.1: After acclimation, one male ("1") was removed from its territory (a), suspended in the air for thirty seconds, and placed into another male's ("3") territory (c) where the antagonistic interaction occurred. The intruder male was then moved back to its original territory (a) and female behavior was recorded for 10 minutes. One male ("2") did not interact but was visible to the test female in territory b, as well as the extra female in territory d. Note: shaded tanks (a', b', c') were used on alternate trials, opaque acrylic partitions were placed between shaded and unshaded compartments used during each trial, and compartment d had an opaque partition between it and compartment a and c'.

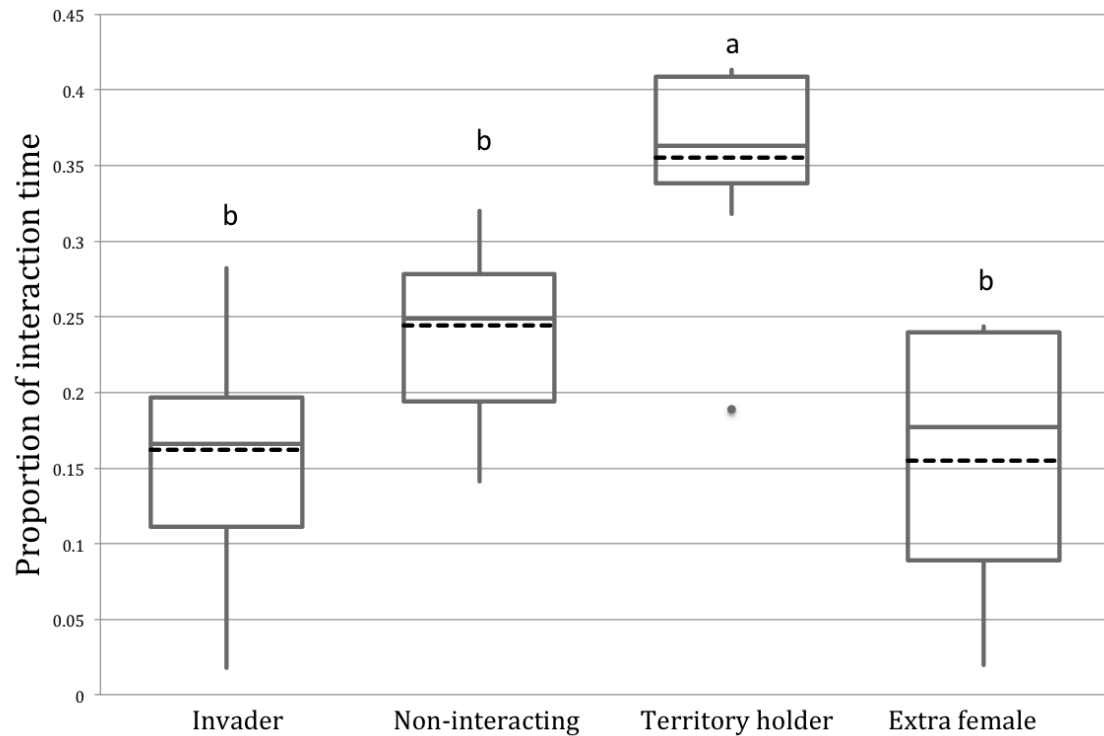


Figure 2.2. Effect of behavioral role on female preference. Of the time that females spent interacting with peripherally-located fish, the largest portion was with males who had been assigned to the winning role. Coefficients “a” and “b” denote significantly different groups as determined by post-hoc analysis. Whiskers represent the upper (75%) and lower (25%) quartiles, boxes the middle (50%) quartile, and outliers are determined by exceeding the 9<sup>th</sup> or 91<sup>st</sup> percentiles, though they were used in the analysis. Median response is represented by the solid line in the box. Dashed lines show sample means.



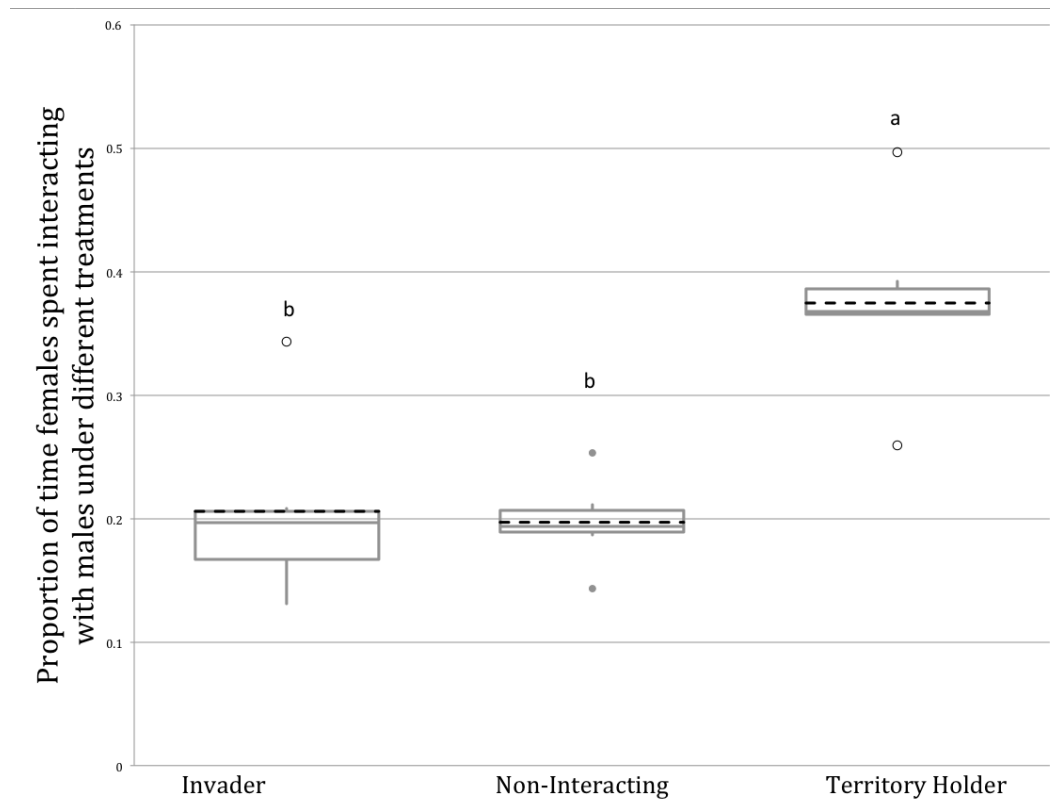


Figure 2.3. Effect of assigned role on male attractiveness. As each male was assigned to each role, its median attractiveness to females varied. Coefficients “a” and “b” denote significantly different groups as determined by post-hoc analysis. Whiskers represent the upper (75%) and lower (25%) quartiles, boxes the middle (50%) quartile, and outliers are determined by exceeding the 9<sup>th</sup> or 91<sup>st</sup> percentiles, though they were used in the analysis. Median response is represented by the solid line in the box. Dashed lines show sample means.

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## CHAPTER 3

### **Within population color-mediated male-male interactions in *Maylandia zebra* (Family *Cichlidae*)**

#### **Introduction**

Species assemblages that are comprised of many closely-related species and differ primarily in male nuptial colors are ideal systems for studying the role of sexual selection in diversification (Panhuis *et al.*, 2001; Seehausen & Schluter, 2004; Genner & Turner, 2005). In contrast to adaptive radiations, we expect that such species assemblages result from differential reproductive success caused by either divergent mate choice preferences or by intrasexual interactions favoring novel types. Furthermore, relatively recently derived and species-rich assemblages are ideal for testing ideas with populations that are in the process of evolving and differentiating (Dijkstra *et al.*, 2007b).

The idea that speciation can be driven by sexual selection is somewhat novel and controversial (Panhuis *et al.*, 2001; Arnegard & Kondrashov, 2004; Coyne & Orr, 2004), despite the theoretical and empirical evidence that sexual selection can increase the rate of speciation (Lande, 1981; Higashi *et al.*, 1999; Seehausen, 2000). However, multiple lines of evidence now point to the role of sexual selection as a primary driver of species divergence. Patterns of male breeding colors across geographic space and phylogenetic relatedness suggest that character displacement occurs through divergent or disruptive selection (Allender *et al.*, 2003), though the

relative importance of female choice and male –male competition on causing such disruptive selection remains unclear. Both aspects of sexual selection, female choice and male-male interaction, are known to reinforce incipient differences between populations that evolve in allopatry before secondary contact (Panhuis *et al.*, 2001). Females will use gross color pattern to distinguish between potential mates instead of phylogenetic relatedness (Jordan, 2008b; Stelkens & Seehausen, 2009) and males, too, will show more aggression to heterospecific males that are more similarly colored to them than towards males that are more closely related, but more differently colored, such as two closely related species or two morphs in the same species that display divergent male nuptial colors (Pauers *et al.*, 2008). Both of these behavioral phenomena occur despite the intermediate ecological specialization and therefore the increased hybrid fitness cost for any offspring that were to result from pairings between more distantly related individuals (McElroy & Kornfield, 1993), further emphasizing the role that nuptial color patterns play in communication between individuals.

Because of these patterns in color and behavior, the *mbuna* cichlids of Lake Malawi are used to study the means by which behavioral interactions could result in evolutionary changes within and between populations (Genner & Turner, 2005). Within the *mbuna*, *Maylandia zebra* (Boulenger) (formerly *Pseudotropheus*) is an especially widespread species complex comprised of a variety of color variations (“morphs”). As maternal mouthbrooders, *M. zebra* females provide all parental investment (Baerends & Roon, 1950; Fryer & Iles, 1972). Males establish, maintain, and defend territories up to about 0.25 m<sup>2</sup> among rocky outcroppings from

conspecific rivals. From their territories, males court females with intricate courtship dances. Females visit multiple territories and mate with a subset of males, resulting in broods with multiple paternities (Kellogg *et al.*, 1995). Only a few examples of females distinguishing between conspecific males are known. These include some preference for increased chroma and contrast (Pauers *et al.*, 2004), and preference for socially dominant behavior (Mellor *et al.*, 2010). Females may mate with any male who meets some minimum threshold of quality or, alternatively, females may only mate with a top proportion of males. If female mate choice is an important force in the diversification of this lineage, the degree to which females distinguish between conspecific males could affect the possibility that sexual selection causes sympatric diversification, instead of merely reinforcing incipient differentiation that arises in allopatry.

It should be noted that color variation occurs not only between species, populations and sexes, but also within individuals over time. Male color is under both hormonal and neural control, and so can change over different time scales because of the effects from stress and dominance status (Seehausen *et al.*, 1999a). Melanophores rapidly expand and contract in response to neural signals and control the barring pattern composed of dark pigmentation on the lateral flanks. In contrast, guanocytes, erythrophores and allophores are under hormonal control and are responsible for the structural and pigment-based blue and red hues displayed by a territorial male (Baerends & Roon, 1950).

The following study aims to answer two questions. First, does color predict an individual male's level of aggression? Second, does the similarity between two males' color predict the amount of aggression shown between those two individuals? To answer these questions, male color will be measured by spectroscopy. Next, each male's aggression towards every other male will be measured. Males will be grouped by the amount of aggression they show and the multivariate color data will be reduced by discriminant function analysis to determine if the group assignments produced by aggression level are similar to the group assignments made from reflectance data.

Next, principal component analysis will be used to determine an index of color similarity between each pair of males and the correlation between that color similarity index and aggressive displays between the same two individuals will be determined.

If males are sensitive to within-population and within-morph color variation, and respond differently to that amount level of diversification, then this sensitivity could provide the selective forces necessary to explain the rapid diversification of this lineage. Until now, the evidence has suggested that males respond to variation that has evolved through the relatively slow processes of genetic differentiation in allopatry, rather than to the more subtle variation found within populations (McCune & Lovejoy, 1998).

## **Methods**

### *Collection and Housing*

Ten males were selected from a lab-reared population of *M. zebra*, F2 from wild-caught individuals. Ancestors of these males were collected from the Mazini reef area of Lake Malawi (14° 05' S, 34° 56' E). Male breeding colors are all blue, with six to eight vertical black bars along the lateral sides. Males were fed once daily and kept on a 12 hour light/dark schedule. Brightly colored, dominant males that were housed with 3-6 other individuals were used for this study.

### *Color measurements.*

Reflectance measurements were taken from the prepectoral patch, approximately 5 mm ventral and 5 mm posterior to the operculum (figure 3.1). This spot was chosen because it is a region of high interspecific color variation (Allender *et al.*, 2003; Jordan *et al.*, 2004). Reflectance measurements were made with an Ocean Optics Jaz spectrophotometer and a tungsten halogen light source, transmitting broad spectrum light from 350-1000 nm. The spectrophotometer was calibrated with a WS-1 white standard, which reflects >98% of light from 220 – 1500 nm. White and dark reference measurements were taken at the beginning of each measurement session. The fiber optic probe was held in place with an aluminum cylindrical probe holder, which blocked outside light from the measurement surface. During each color measurement, a fish was held against an optically pure section of glass. Raw reflectance data taken from the wet surface of the fish ( $R_{\text{wet}}$ ) were converted into submerged reflectance measurements



( $R_{\text{submerged}}$ ) using Duntley's (1960) formula that relates the two measurements:

$$R_{\text{submerged}} = \frac{R_{\text{wet}}}{(0.564 + 0.42 * R_{\text{wet}})}$$

This formula assumes the angle of measurement to be 90°, which dictated the use of the cylindrical probe holder.

Males were measured as quickly as possible in order to accurately measure the color of each individual in its unstressed state. If a measurement took longer than 3 minutes to complete, the male was returned to its housing tank and the measurement was reattempted no less than 24 hours later.

#### *Analysis of color data*

The mean reflectance measurements from 19, 20nm-wide bins across the cichlid visible spectrum of 350 to 650nm (Carleton *et al.*, 2000; Sabbah *et al.*, 2010) were used in the principal components analysis. The difference index between each individual was calculated as the Euclidian distance between the principal component scores for each individual (Endler, 1990; Armenta *et al.*, 2008). A score of zero indicated no difference. Difference indices were calculated using multiple combinations of PC scores as determined by the 1) amount of variation explained by each principal component and 2) the chromatic characteristic that each principal component described (Cuthill *et al.*, 1999).

For reference, the ten individuals from the current study were compared with a sample of four individuals from three different color variations of *M. zebra* that display different nuptial coloration to determine whether color measurements

can group individuals by population. One male was a “barless” variety of *M. zebra* that showed all blue coloration. Two others were similarly “barless” and showed orange color patterns. The last was a barred male showing orange patches around the prepectoral patch and red coloration on the dorsal fin.

### *Aggression measurements*

Each male was allowed to establish a territory in a 39 l tank with a transparent acrylic divider that divided the tank in two parts along its longest axis, approximately one quarter the length of the tank, leaving a 29 l volume for the residential male and approximately 10 l for the intruder’s compartment (figure 3.2). Males were allowed to establish a territory for at least 24 hours before an intruder was introduced to the adjacent compartment. Through trial and error, this period was found to be sufficient for males to exhibit territorial behaviors, such as defending the territory from intruders and maintenance of the territory by manipulation of the rocky substrate surrounding the cave-like, stone habitat. The habitat construction was informed by field observations, which suggest that cave-like territories are preferred by both males and females, as inferred by territory establishment and number of female visits (Jordan *et al.*, 2010). When an intruder was placed in the adjacent compartment, interactions were recorded on video in a secluded area free of visual contact from researchers. The time that the resident male spent in contact with the acrylic partition attempting to “butt” or “bite” the intruder was used to measure the amount of aggression shown by the resident

towards the intruder, as these displays are known aggressive behaviors (Baerends & Roon, 1950).

### *Statistical analysis*

Between-male variation in aggressive response was investigated through ANOVA. Post hoc analysis was used to compare differences between each male with the least significant difference test (Fisher, 1925). The results of the post-hoc analysis were used to place individuals into distinct categories of aggressiveness from highly aggressive to less aggressive. These categories were then used in a discriminant function analysis with the multivariate color data described above to determine whether differences in reflectivity can be used to predict male aggressive behavior.

As some males are inherently more aggressive than others, each aggression score was divided by that individual's mean aggressive response. The time spent "butting" and "biting" the acrylic partition in each trial was standardized to that male's inherent level of aggression by dividing the mean of all of that male's "butting" and "biting" times. This score was then log transformed in order to normalize the data for linear regression, which was used to investigate the relationship between color similarity and aggression.

## **Results**

### *Reflectance spectra*

Visual inspection of reflectance spectra reveals an obvious degree of variation between males (figure 3.3). The reflectance spectra varied in both total percent reflectance and as well as in the shape of each spectrum. Principal component 1 explained 87.3% of the total variation between males, PC 2 explained 10.9%, and PC 3 explained 1.5%. The principal component coefficients for PC1 were uniformly positive and high in magnitude (figure 3.4), suggesting that PC1 captured variation in brightness across the visible spectrum of the fish (Cuthill *et al.*, 1999). As such, PC1 will be referred to as the “brightness variation” axis. The principal component coefficients for PC2, on the other hand, were large in magnitude and positive between 350 nm and about 420 nm, and large in magnitude and negative from about 520 nm and higher. This suggests that PC2 represents variation in the relative amount of short-wavelength to long-wavelength reflectance. Therefore, it will be referred to as the “UV-red variation axis.” Finally, the principal component coefficients of PC3 are positive below 400 nm and above 550 nm, which suggests that PC3 represents variation in the relative amount of medium wavelength reflectance in relation to the two extreme ends of the visible spectrum. As such, PC3 will be named the “blue versus red and UV” axis.

Plots of individuals used in the study population based on their PC scores (diamonds in figure 3.5) show that the amount of variation within the population appears overlaps with the reference reflectance spectra of individuals from closely relate populations showing different color patterns (triangles and squares, figure 3.5).

### *Color and male aggression*

A wide range of aggression was observed between males (figure 3.6). Analysis of variance revealed significant differences between males (table 3.2). Post-hoc, pairwise analysis was conducted with the least significant difference test (i.e. Fisher's LSD test). Males were grouped by aggressiveness prior to discriminant function analysis using the results of the post-hoc analysis from the analysis of variance. Males were grouped into three categories 1) those that were significantly more aggressive than the least aggressive males, 2) those that were not significantly different than either the most or least aggressive males and 3) those that were significantly less aggressive than the most aggressive males. Using these grouping variables and the multivariate reflectance data from each male, discriminant function analysis placed eight of the ten males into the same aggressiveness categories by using the reflectance data. Two of the six males that were ranked with the least aggressive group based on behavioral data were regrouped with the "medium" aggressive group by the discriminant function analysis based on the reflectance data. The eight other males were clumped with their original behavioral group using the reflectance measurements. The following weightings were assigned to each variable and used to discriminate between the three groups: -9.422 for function 1 and 3.169 for function 2 at 360nm, 28.082 and -4.65 for 380nm, -23.807 and 3.09 at 400nm, and 5.726 and -1.212 at 460 nm. The centroid for the most aggressive group were 3.235 for function 1 and -.075 for function 2, for the

moderately aggressive group the centroids were -0.45 and 0.657, and for the least aggressive group the centroids were -0.928 for function 1 and -0.194 for function 2.

### *Color similarity and male aggression*

There was a significant, negative correlation between the amount of aggression shown by a resident towards an intruder and 1) the color similarity index calculated by using the “brightness and UV/red” axes (PC1 and PC2) in combination ( $r^2 = 0.06$ , 81 d.f.,  $p = 0.03$ )(figure 3.7) as well as 2) the color similarity index calculated by using just the “UD/red” axis (PC2) ( $r^2 = 0.05$ , 81 d.f.,  $p = 0.04$ ). In other words, males showed significantly more aggression towards intruders who were more similarly colored than towards males who were less similarly colored. There was no significant relationship between the color similarity index calculated using the “blue versus red and UV” axis (PC3) and aggression ( $r^2 = 0.03$ , 81 d.f.,  $p = 0.09$ ) or by using the “red versus UV” and “blue versus red and UV” axes (PC2 and PC3) in combination and aggression ( $r^2 = 0.02$ , 81 d.f.,  $p = 0.21$ ). In other words, males did not discriminate between rivals who varied primarily in the relative amount of blue light reflected on their prepectoral patch.

## **Discussion**

Two notable findings emerged in this study. The first was that aggressive males can be distinguished from less aggressive males using spectral data. This result is expected based on behavioral studies that describe the change in color that males undergo over short and long timespans based on neural and hormonal changes as males establish and defend territories (Seehausen *et al.*, 1999b). Also,

since most of the variation in spectral data is in total brightness of males and it is the brightness that changes when males become territory holders (Holzberg, 1978), it is expected that this characteristic of light would be used to discriminate more aggressive males from less aggressive ones.

The second finding was that there was a significant, linear relationship between the color similarity index and the amount of aggression shown towards a rival male. The linear relationship between color similarity and the amount of aggression displayed towards rivals from within the same population of *M. zebra* is similar to the relationship seen in between-species experiments and field studies. Furthermore, the distinction that males make between rivals occurs in this study at a much more subtle color scale than previously thought. This also suggests that males are more sensitive to subtle color variations found within a single morph than previously demonstrated in interspecific experiments, such as in Pauers (2008) and Dijkstra (2007b).

Two relationships were found to predict aggressive displays between males: 1) the color similarity index created with both variation in brightness and red versus blue (PC1 and PC2) and 2) the color similarity index created by using just the red versus UV variation (PC2). Though variation in blue versus red and UV reflectivity (PC3) did not predict the aggression shown between two males as expected, this is likely because so little variation was found on the third principal component axis (1.5% of the total amount of variation).

Sexual selection has long been invoked to explain the spectacular array of male nuptial colors among the *mbuna* cichlids. Indeed, the pattern by which male nuptial colors are found in geographic and phylogenetic proximity strongly suggest that there is a competitive exclusion force driving the rapid diversification of this lineage (Allender *et al.*, 2003), though divergent female choice or male-male competition could both explain this pattern. As such, the relative importance of male-male competition and female choice are disputed, with both forces invoked to explain the evolution of these populations. Females are known to distinguish between males of closely related species using visual cues (Jordan *et al.*, 2003; Knight & Turner, 2004) as well as a combination of visual and other cues (Blais *et al.*, 2009). Furthermore, there is evidence that females distinguish between conspecific males by more than simple territory establishment (Pauers *et al.*, 2004).

Others have suggested, however, that male-male competition is the likely driver of species differentiation (Seehausen & Schluter, 2004). Experimental evidence backs up this assertion (Dijkstra *et al.*, 2007b; Pauers *et al.*, 2008), at least in regards to males that have already differentiated in allopatry.

The way in which male-male competition was thought to promote speciation in this and similar systems is through the competitive advantage that rare color morphs enjoyed in establishing territories in space-limited rocky outcroppings (Seehausen & Schluter, 2004). However, such models of diversification did not address the selection pressure required for the origin of novel color patterns. Instead, these models relied on the formation of novel color patterns in allopatry



and the reinforcement of nascent species boundaries upon secondary contact between recently differentiated morphs. The results of this study suggest that the selection pressure for the origin of distinct color patterns lies within the potentially heritable color variation present within a single population of individuals who look superficially similar to one another, i.e., who belong to the same color “morph.”

The mechanism by which differently-colored males would enjoy a selective advantage is the same as was suggested by Seehausen and Schluter (2004), differently colored males would be the object of less aggression than males who are similarly colored to the population average. One crucial assumption of this model that has not yet been tested is the degree to which such males are able to attract mates. Given that males are more sensitive to within population color variation than previously suggested and the fact that females may likewise be quite sensitive to within species color variation (Pauers *et al.*, 2004), this assumption deserves attention.

Male-male interactions male play an important role in the diversification of this species-rich assemblage. This study provides a mechanism by which selective forces may act in order to create the observed patterns of male nuptial color diversity. Until this point, explanations for diversity have relied on the emergence of novel color patterns in allopatry with reinforcement during secondary species contact. The degree to which such subtle color variation is heritable must be established before the effect that such patterns of behavior can have on diversification is known.

ANOVA						
Source of Variation	d.f.	SS	MS	F	p-level	F critical
Between Groups	9	775,188	86,132	3.807	< 0.001	2.386
Within Groups	72	1,628,826	22,622			
Total	81	2,404,015				

Table 3.1: Results of the ANOVA using individual male aggressive responses to introduced rival males. There was a significant difference between the amount of aggression displayed, necessitating the use of each male's average aggressive response to normalize aggressive scores.

## Figures

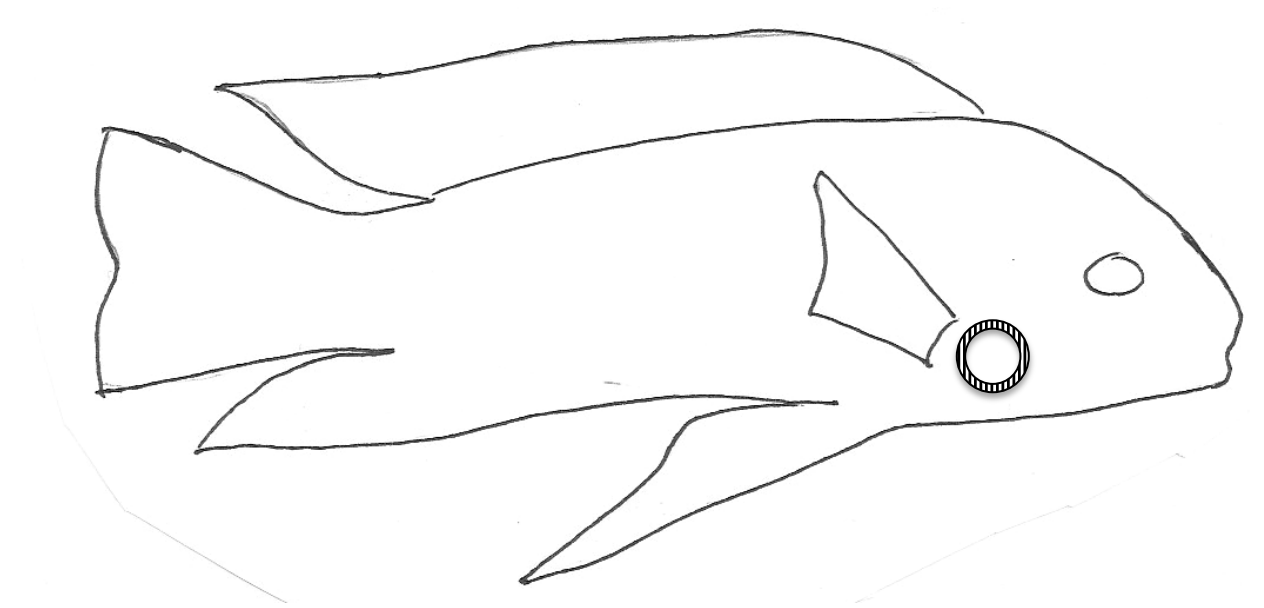


Figure 3.1. Location of reflectance measurement notated by hatched circle.

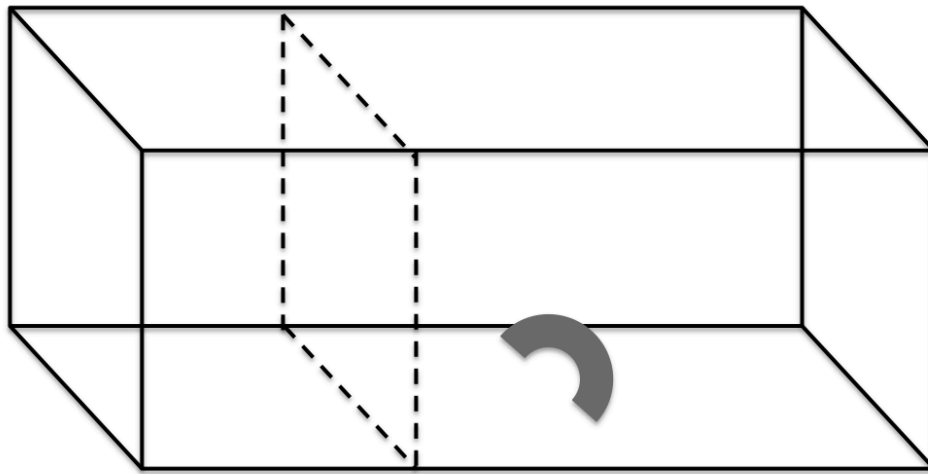


Figure 3.2. Males were placed in the right half of a divided tank and permitted to establish territories for 24 hours prior to the introduction of an intruder in the left chamber. Males were separated by a transparent acrylic divider to prevent injury. Time spent “biting” and “butting” the acrylic divider by the resident was recorded.

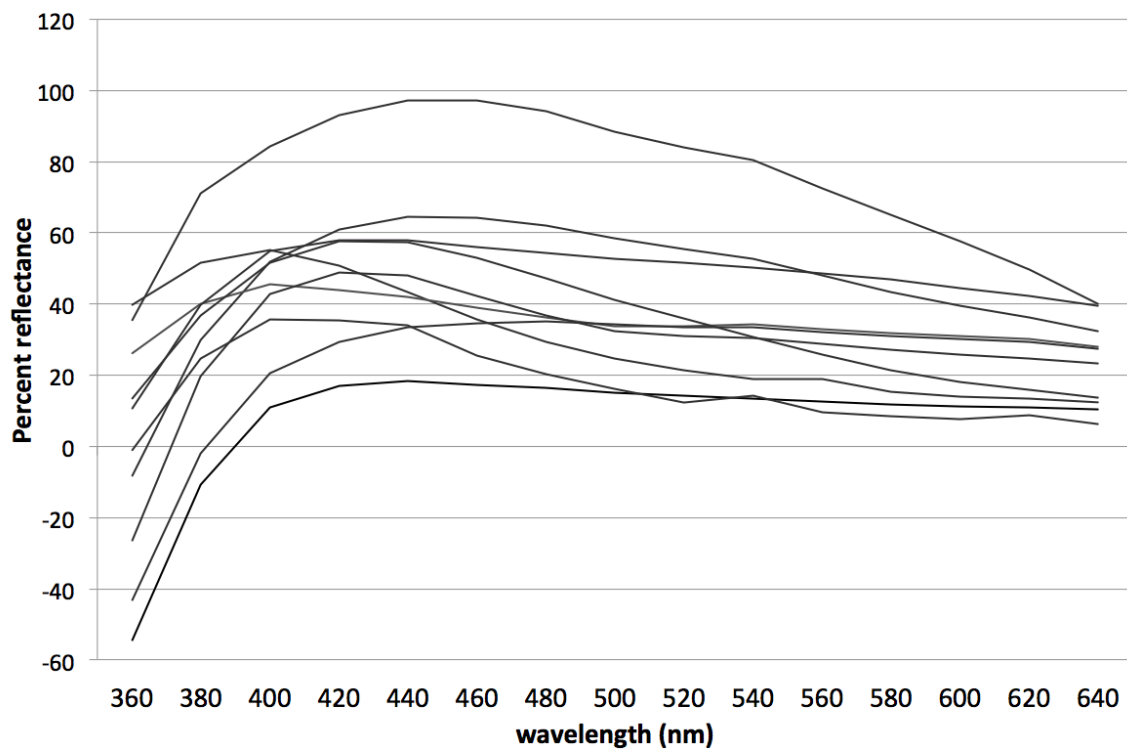


Figure 3.3. Reflectance spectra of the ten focal males. Note the wide range in the total reflectance of each spectrum, which is the total brightness of a male. This character is represented primarily in PC1, whereas PC2 and PC3 represent other color data, such as hue and chroma, as represented by the shapes of each curve.

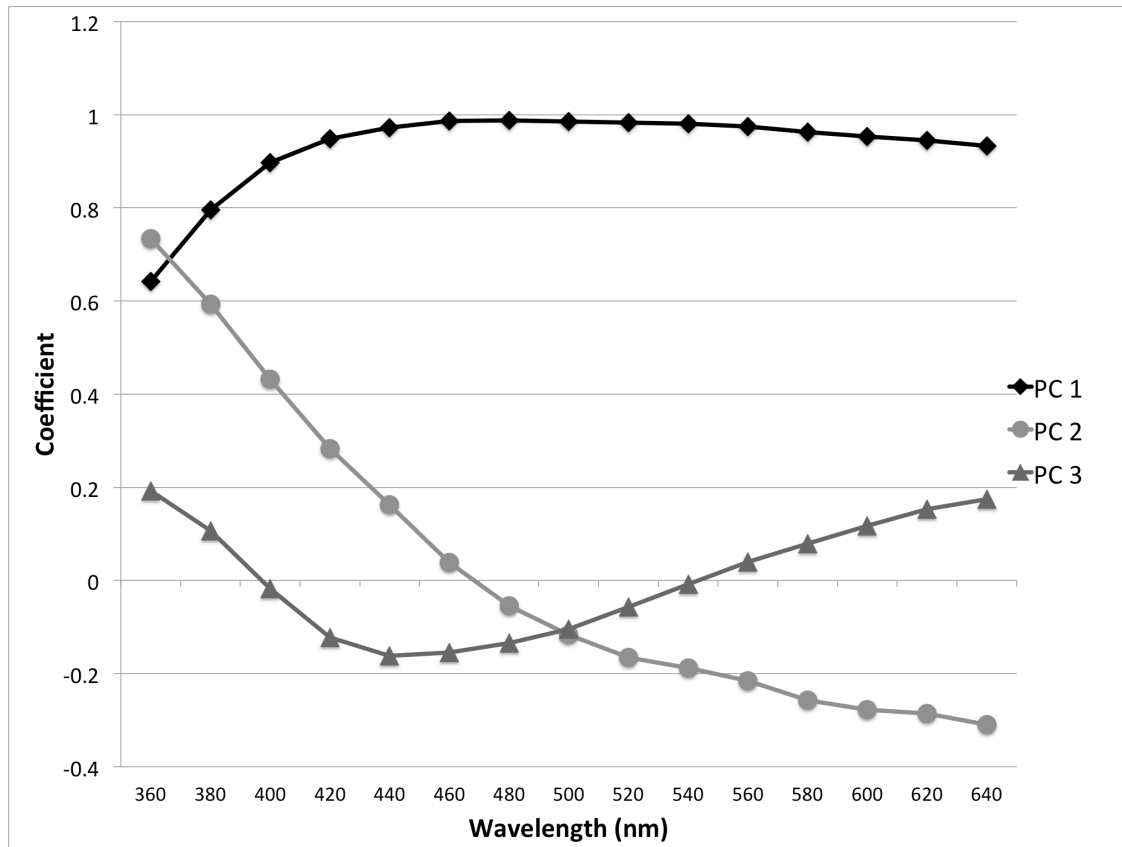


Figure 3.4. Graphical representation of the component matrix obtained through PCA of the ten focal males. Almost all wavelengths weight highly and positively on PC1, suggesting that it represents variation in brightness between individuals. Variable weightings for PC2, which accounts for 10.9% of the total variation, are high in magnitude at both ends of the visible spectrum, but in different directions, suggesting that PC2 represents variation in the relative amount of red to UV light. Finally, PC3, which accounts for 1.5% of the total variation, has variable weightings that are large in magnitude around 450 nm (blue light) but positive in most other wavelengths.

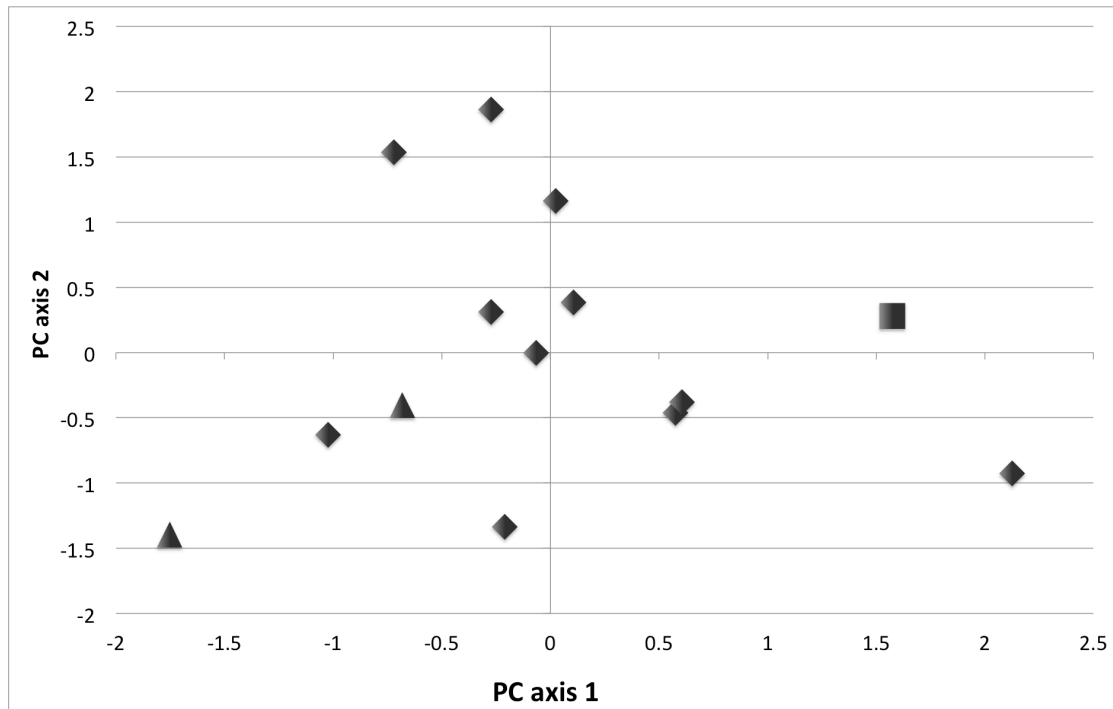


Figure 3.5. A plot of individuals according to their principal components 1 and 2. Brightness weighs heavily on PC1, whereas PC2 represents the relative amount of red to UV reflectivity. Study males are represented by diamonds. Representative males from closely related populations with the red morph are shown by triangles, all blue ("barless") by a square.

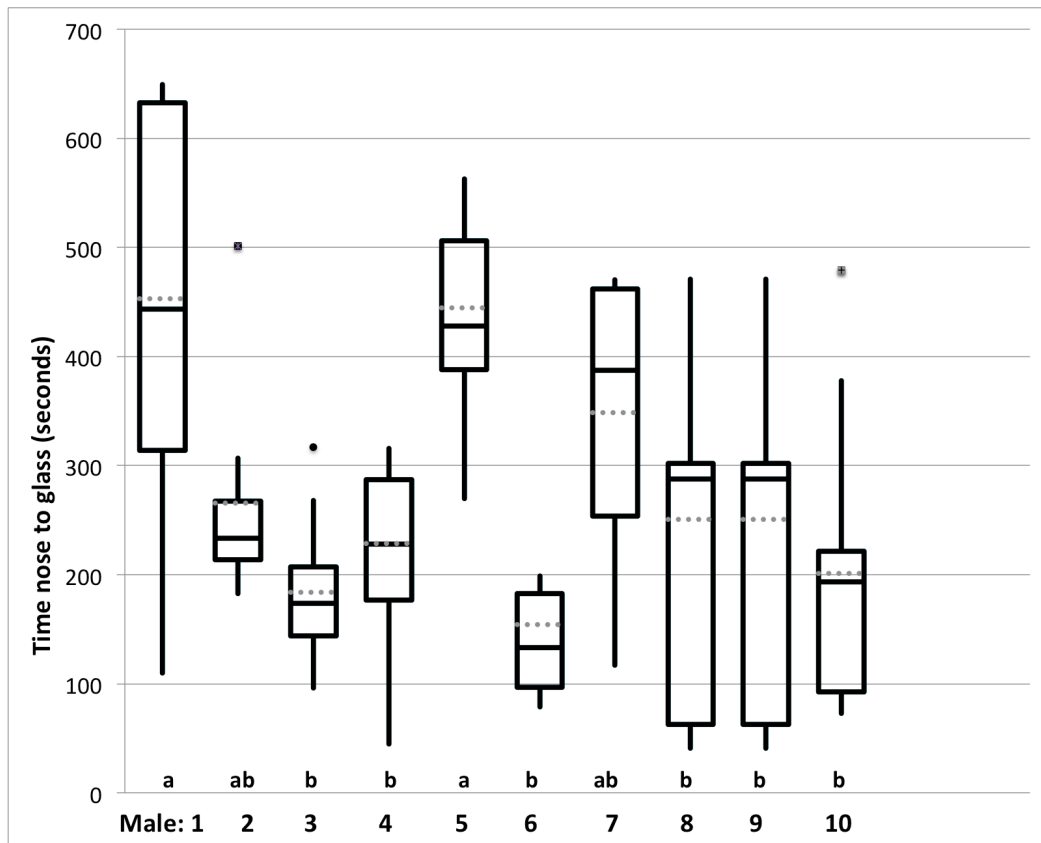


Figure 3.6. Box plots showing lower, median and upper quintile of each male's aggressive responses to intruder males. Post-hoc analysis reveals differences between the levels of aggression shown between males (grouped by letters a, b, and ab). Whiskers represent the upper (75%) and lower (25%) quartiles, boxes the middle (50%) quartile, and outliers are determined by exceeding the 9<sup>th</sup> or 91<sup>st</sup> percentiles, though they were used in the analysis. Median response is represented by the solid line in the box. Dashed lines show sample means.



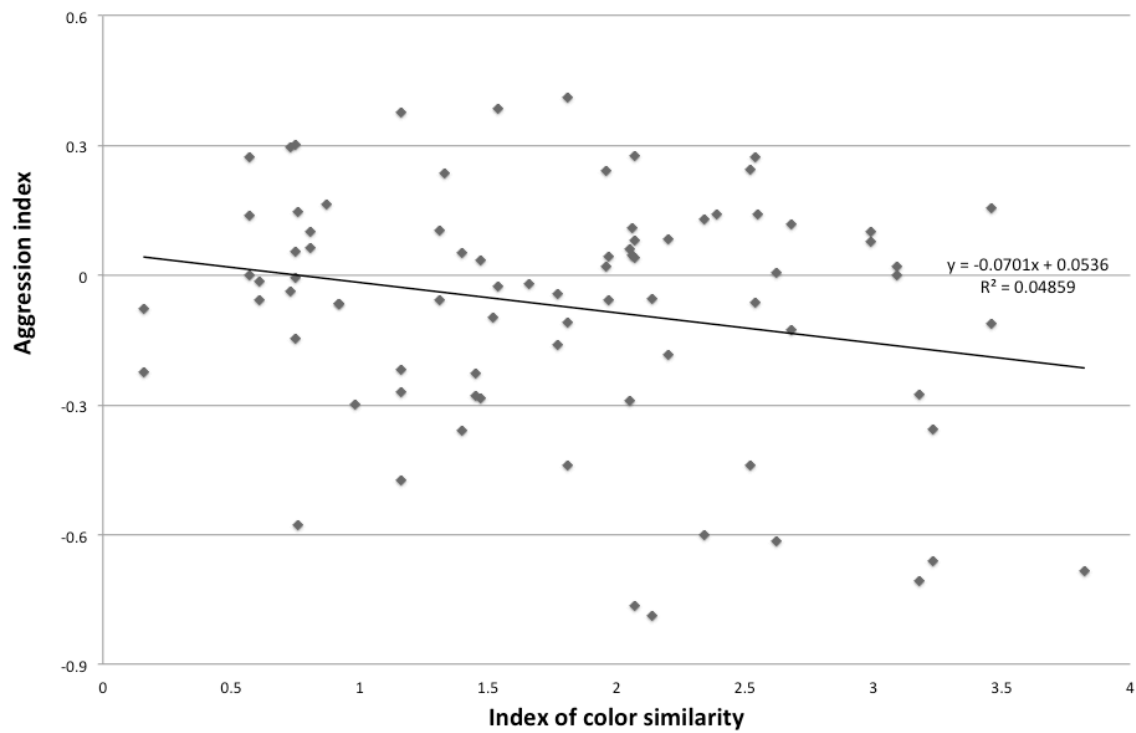


Figure 3.7. There is a significant, linear relationship between color similarity and the amount of aggression displayed towards a rival. More aggression (higher on vertical axis) is shown to more similarly colored rivals (closer to 0 on the horizontal axis).

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## CHAPTER 4

### Reproductive Success on a Simulated Lek Environment

Young species assemblages comprised of unusually high numbers of species beg the following question: what forces are affecting the rapid diversification of this lineage? Such species radiations are widely used for studying speciation because of the increased probability of capturing processes that have recently caused population divergence (Coyne & Orr, 2004). Though barriers to gene flow can evolve for a variety of reasons, sympatrically-differentiating lineages are thought to require a force causing divergent selection by selecting for extreme phenotypes or penalizing those close to the population mean. The rapidly diverging *mbuna* species complex of Lake Malawi is an ideal lineage for studying these evolutionary processes, especially the role of sexual selection in driving divergent selection within populations (Genner & Turner, 2005).

The emerging consensus regarding the role of sexual selection in the diversification of this rapidly evolving group of fishes is that a combination of male-male competition and female choice is responsible for the relative success of newly established male nuptial colors. The pattern of male nuptial colors over geographic and phylogenetic space shows that similarly-colored males tend to evolve repeatedly in distantly-located populations (Allender *et al.*, 2003). Seehausen and Schluter (2004) suggested that males are likely to direct more aggression towards similarly-colored heterospecific rivals because those males are superficially more

similar to their actual conspecific rivals, despite the fact that gross color pattern is a poor predictor of phylogenetic relatedness. This pattern of behavior was confirmed by experimental investigation (Pauers *et al.*, 2008). Likewise, females use gross color patterns more so than phylogenetic relatedness (Jordan, 2008b; Stelkens & Seehausen, 2009), despite the higher risk of hybrid fitness cost because of ecological niche specialization.

One question that remains is whether or not the initial stage of divergence within a single population is because of behavioral interactions mediated by subtle color variations. The contrasting scenario, and the null hypothesis given the evidence required to accept sympatric speciation, is that differentiation occurs in allopatry because of genetic drift and that incipient species differences are reinforced by patterns of behavior (i.e., male-male competition or female mate choice) upon secondary contact.

In order to investigate the above questions one must explore the factors that affect differential reproductive success in this lineage. The following study examines the role of territory establishment, male-male interactions, and color on the reproductive success of a group of males from the *Maylandia zebra* (Boulenger) species complex. Males were ranked by aggression using short, intensive male-male contests. Their color was then measured through spectroscopy. Males were then permitted to establish, maintain and defend territories in a 4500 l pool. Next, females were introduced and after three months any surviving offspring were sacrificed for paternity analysis. The degree to which color and territory

establishment and placement correlates with reproductive success were then measured.

## **Methods**

### *Housing*

Ten size-matched males were selected from a population of second and third generation descendants from wild-caught individuals collected near the Mazini reef area of Lake Malawi (14° 05' S, 34° 56' E). Fish were kept on a 12 hour light-dark schedule, with a one hour period of subdued lighting at “dawn” and “dusk.” Fish were fed once per day. Individuals were kept in isolated, 10 l tanks for at least one month prior to the start of experimentation.

### *Male-male aggression measurements.*

Before being placed into the mating arena, males were ranked based on three rounds of male-male aggression trials. In each trial, ten males were placed in a 38 l tank with one cave-like territory. Territory configuration was informed through field observations, during which female preference was scored through visitation counts (Jordan *et al.*, 2010). A male was removed from the tank upon successfully defending the central territory for a minimum of two minutes from all intruders.

One trial of measurement was completed once nine males successfully established and defended the central territory, with the last male being ranked 10<sup>th</sup>.

### *Color measurements*

A spot on the prepectoral patch was used for obtaining the reflectance measurement approximately 5 mm posterior and 5 mm ventral to the operculum. This spot was chosen because it is a region of high color variation between species (Allender *et al.*, 2003; Jordan *et al.*, 2004). An Ocean Optics Jaz spectrophotometer and a tungsten halogen light source transmitting broad spectrum light from 350-1000 nm were used for reflectance measurements. The spectrophotometer was calibrated with a WS-1 white standard. The white standard reflects more than 98% of light from 220 – 1500 nm. Dark and white reference measurements were taken at the beginning of each measurement session. The fiber optic probe was held in place with a cylindrical probe holder in order to block outside light from the measurement surface. During each color measurement, a fish was held against a section of glass that transmitted close to 100% of light from across the UV to infrared spectrum. Duntley's (1960) formula was used to relate the reflectance measurements from the wet surface to the equivalent measurement taken at depth:

$$R_{\text{submerged}} = \frac{R_{\text{wet}}}{(.42 * R_{\text{wet}} + .564)}.$$

### *Establishment of breeding arena*



Males were placed into a 4500 l pool (figure 4.1) that contained seven territories composed of shale cave formations approximately 200 mm in diameter and 50 high. The degree to which each territory was preferred was measured by the presence of males in each territory over the course of the first hour. Males were scored as having established territories in preferred sites, non-preferred sites (i.e. ones in which no other male was located) or as having not established a territory. Territoriality was measured 48 hours after introduction to the pool. After territoriality was measured, 10 females were introduced to the arena. Fish were fed once per day with sinking pellets to allow males to stay on their territory. Broad spectrum lighting was maintained on a 12 hour light/dark schedule, with a 1 hour period of intermediate lighting at dawn and dusk.

#### *Paternity assignment*

After 85 days, all resulting offspring were collected for paternity analysis. The offspring living at 85 days may represent a non-random sample of total offspring sired, with an expected bias towards the earliest spawning. This is because of predation by the earliest offspring of the later fry.

Each male and each offspring from the pool was fin clipped for paternity testing. A small section of anal fin, approximately 25 mm<sup>2</sup> was cut from each fish and placed in 99% ethanol in individual vials for DNA analysis. Chelex methodology was used to extra DNA, as in Estoup, *et. al.* (1996). Offspring paternity assignment was made using four loci. The loci used were: PZE-85, UNH-002, UNH-017, and UNH-001 (Kellogg *et al.*, 1995). In order to amplify the necessary loci, polymerase chain

reaction (PCR) was used as described by Ayllon *et. al.* (2004). If paternity was uncertain because of shared alleles, paternity assignment was determined by maximum likelihood. The program CERVUS was used to assign paternity based on offspring genotype, which was determined by maximum likelihood. Male reproductive success was measured by total number of offspring and by proportion of all offspring analyzed.

### *Statistics*

A principal components analysis was performed in order to qualitatively distinguish reproductively successful males from those that were less successful based on color measurements. A discriminant function analysis was performed in order to determine if highly successful males could be distinguished from those males who sired few or no offspring. Likewise, the establishment of territories between reproductively successful and unsuccessful males was also compared. The following comparisons were made: reproductive success (RS) of territorial versus non-territorial males; RS of males in preferred territories, non-preferred territories, and non-territorial males; and RS of males defending centrally located territories versus peripherally located territories.

## **Results and Discussion**

### *Male territory establishment*

The three territories located closest to the center of the mating arena were the focus of all 43 observed male-male contests. Though males were introduced to

the pond along its edge, all individuals moved to the centrally located territories, including the territory established at the filter intake assembly. The observed preference for centrally located territories could be the result of male competition for sites where females are most likely to visit based solely on random movement across a lek, in other words the “hotspot” hypothesis (Bradbury & Gibson, 1986).

### *Color Measurements*

The first principle component from the reduced reflectance data accounted for 70.9% of the total variation. Weightings from PC1 were uniformly high in magnitude and positive (figure 4.2) over the entire visible spectrum, suggesting that PC1 described variation in brightness between males. PC2 accounted for 24.2% of the variation and was large in magnitude at the purple/UV and red range of the spectrum, but opposite in sign at both ends, suggesting that PC2 accounted for variation in the relative amount of purple and UV reflectance versus red. PC3 accounted for 3.8% of the variation in the multivariate reflectance data and was negative around 500nm but positive around the UV and red range of the spectrum, suggesting that PC3 accounted for variation in the relative amount of blue to UV/red light.

### *Paternity Results*

Paternity was assigned with 100% certainty for 17 of the 26 offspring. For the remaining offspring, paternity was assigned based on maximum likelihood. Reproductive success for a male ranged from 0 to 10 offspring (figure 4.3). The two males with the highest reproductive success accounted for more than 60% of all

offspring (figure 4.4). The reproductive success of territory holders was not significantly different from non territory holders (Mann-Whitney U Test:  $N = 10$ ,  $Z = 0.735$ ,  $P > .05$ ). Median dominance rank did not correlate with reproductive success (Kendall Tau:  $N = 10$ ,  $\tau = 0.11$ ,  $P > .05$ )(figure 4.5). Males in territories where contests were observed did not have higher reproductive success than those in non-preferred territories or those males who were not observed defending a territory (last two categories pooled; Mann-Whitney U Test:  $N = 10$ ,  $Z = 0.645$ ,  $P > .05$ )(figure 4.5). The “preferred” (i.e. contested) and the “centrally located” territories were the same group of territories, so no additional comparison was made.

### *Color*

Reproductively successful males separated on the second principal component axis (figure 4.6). This axis represented the variation in reflectance in UV and purple versus red wavelengths. Their lower scores on PC2 suggest that these males were “redder” than less reproductively successful males. The fact that redder males were more successful in reproduction has theoretical support found in literature regarding carotenoids, honest signaling, and sexual selection (see discussion in Kodric-Brown (1985)). Discriminant function analysis revealed that one male could not be correctly placed into the “highly successful males” by using the reflectance data, whereas all of the “less successful males” were correctly placed in that category based solely on the reflectance data.

Paternity assignments reveal a surprising complicating factor: territory establishment is not necessary for males to reproduce successfully. This could be for

a variety of reasons. The first is the possibility for sneaker males to successfully fertilize eggs during courtship between two other individuals, which is known to occur in the cichlid species flocks of other African great lakes (Kuwamura, 1987), but is not a known strategy within this group (Parker & Kornfield, 1996). Given that these fish use external fertilization, sneaker male strategies should be relatively widespread. A second explanation is that the traits that enhance competitiveness in male-male contests are not associated with the signals females use to evaluate potential mates. This is unlikely, as the outcomes of male-male competition can positively affect female mate choice (Mellor *et al.*, 2010), though it is possible that extremely aggressive territory defense could be unilaterally applied to visiting fish of both sex.

In order to determine the degree to which variation in reproductive success can account result in disruptive selection, further trials need to be conducted. If sexual selection is driving sympatric populations apart by either male-male competition or female mate choice, then one would expect to find that males displaying nuptial coloration at either end of the spectrum measured in a population would be expected to achieve the highest degree of reproductive success. This could be because such males are allowed to establish territories free from harassment of other males, or possibly because of diverging female preference for male nuptial colors.

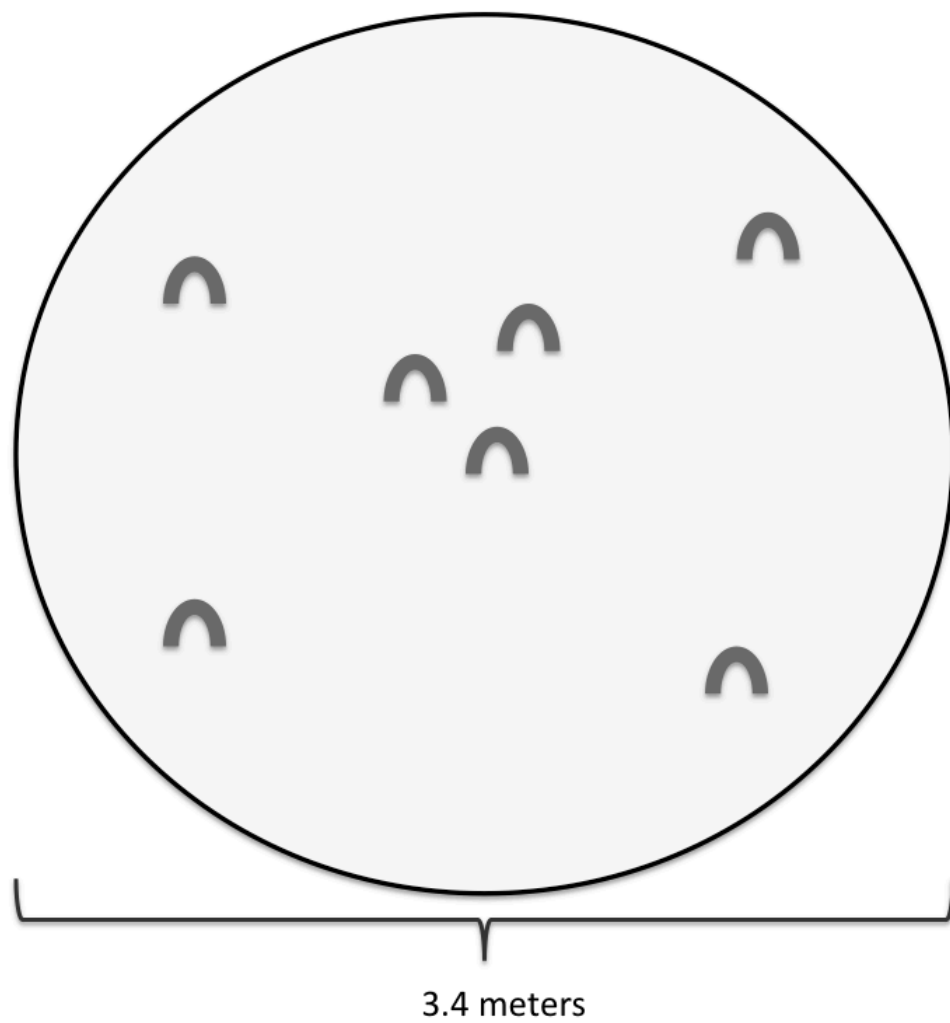


Figure 4.1. Arrangement of territories in pond. All observed territory contests occurred in the central three territories.

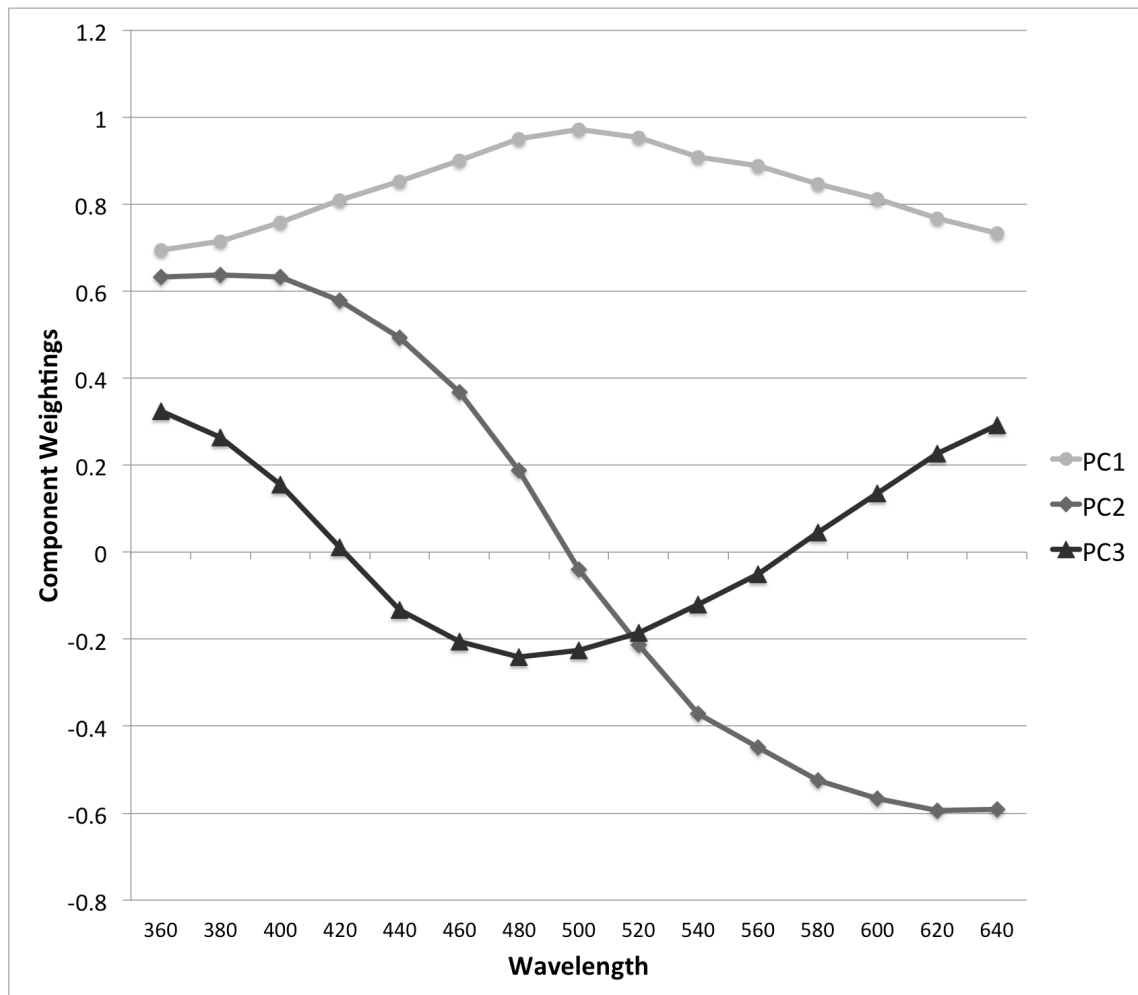


Figure 4.2. Weightings of each factor based from principal components analysis.

Note that PC1 is uniformly large in magnitude and positive, suggesting that it represents variation in male brightness. PC2 is large in magnitude at the extreme ends of the visible spectrum, suggesting that it represents variation in the relative amount of UV/purple to red light. PC3, representing about 3% of the variation, represents variation in the relative amount of blue light versus light from the extreme ends of the visible spectrum.

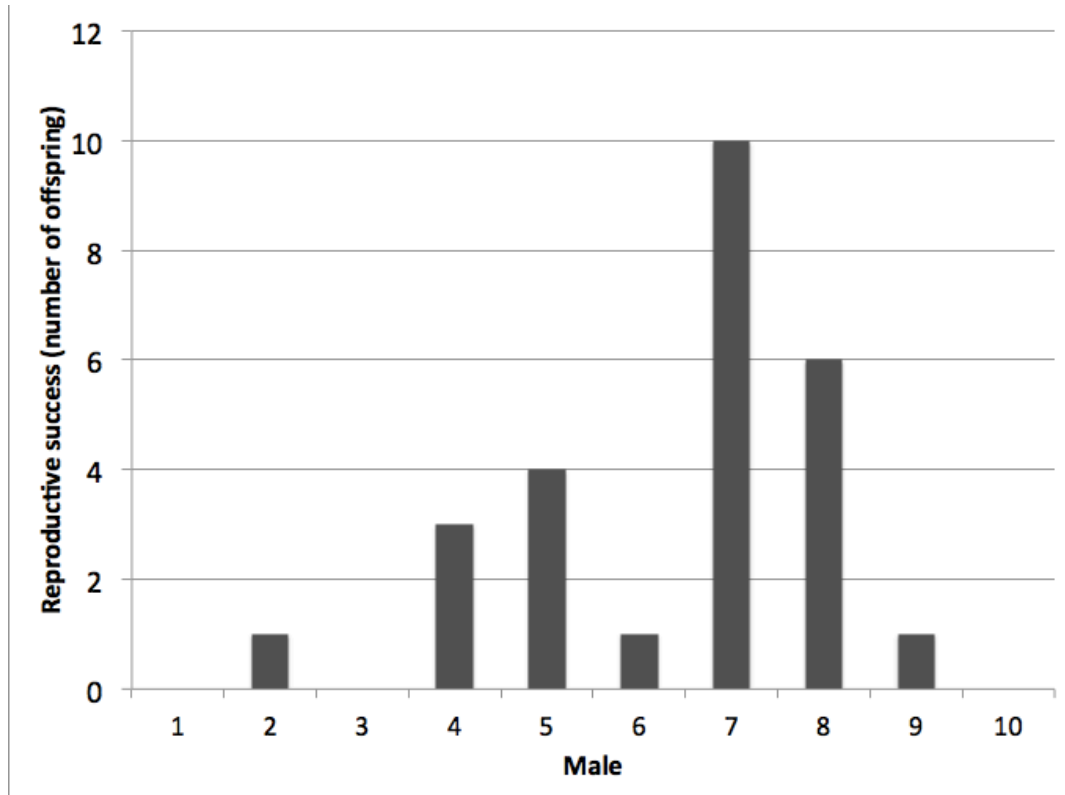


Figure 4.3. The number of offspring of each male. Note the wide range in male reproductive success.



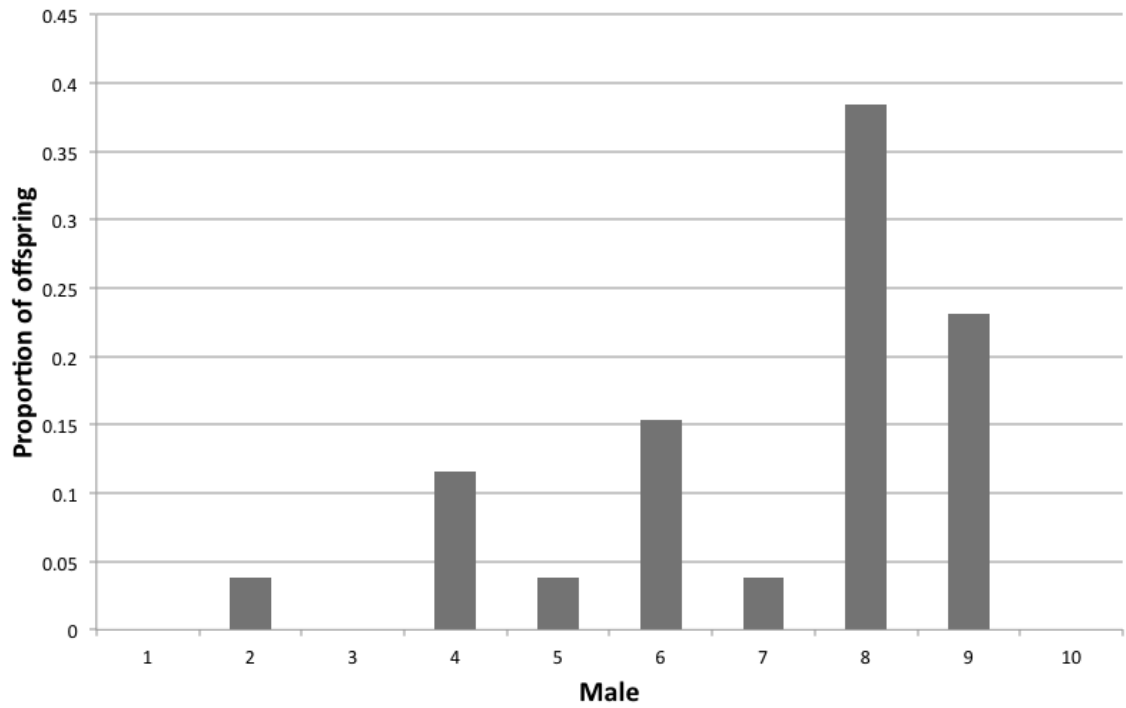


Figure 4.4. The proportion of all offspring of each male.

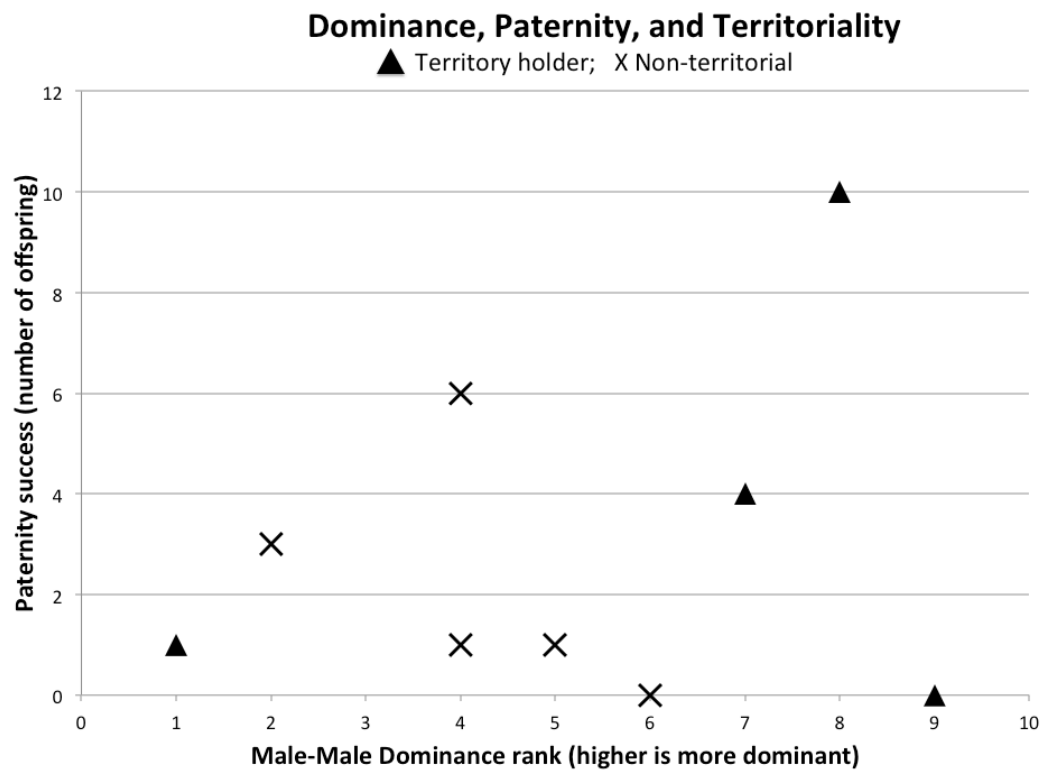


Figure 4.5. The reproductive success of males versus the score they received in male-male competition contests. Note that territory establishment does not predict reproductive success, either.

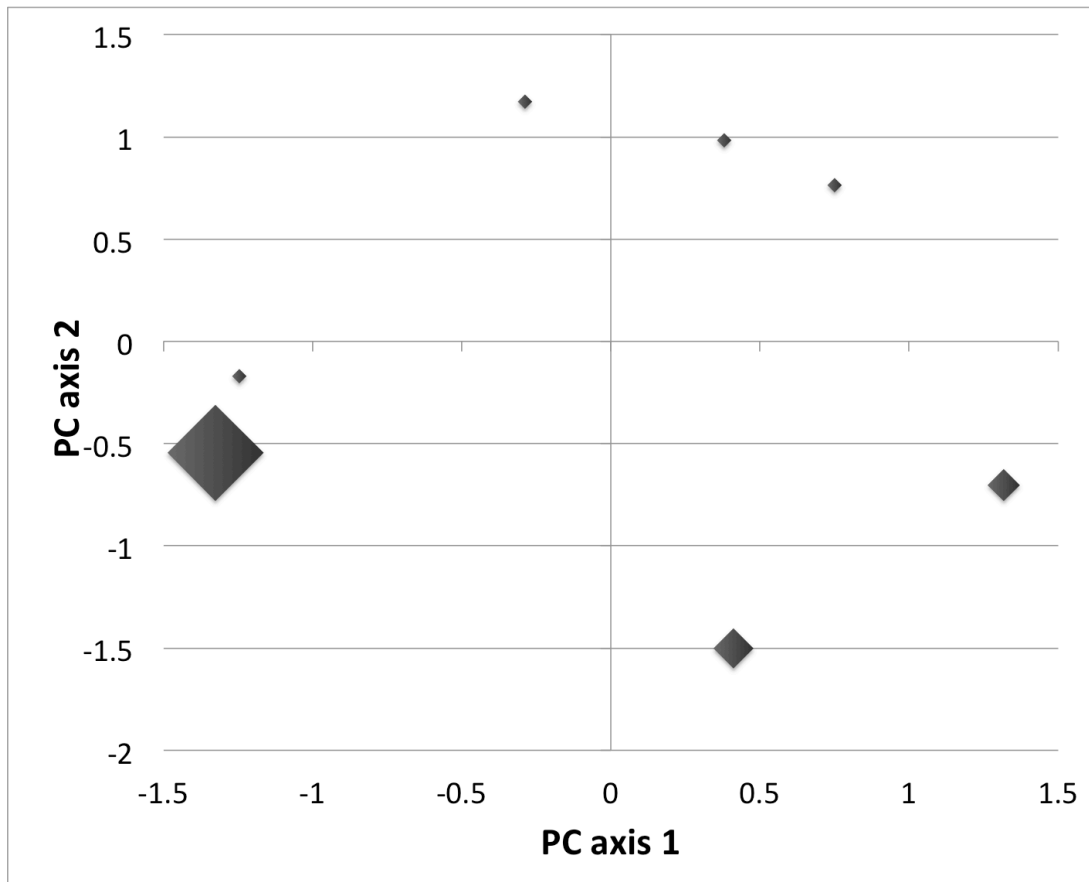


Figure 4.6. Male reflectance measurements were reduced in a principal components analysis. The first principal component account for 70.9% of the variation and described the “brightness” of each male. PC2 account for 24.2% of the variation and described the “hue” of the individual, specifically the amount of red light reflected compared to the amount of UV and purple light reflected. Diamond size is proportional to an individual’s reproductive success. Males separated by RS along the second principal component: males with a higher RS ranked lower along the second principal component, suggesting that they were redder than the less successful males.

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## SECTION II

### CHAPTER 5

#### TROUBLED TRANSITIONS INTO COLLEGE AND THE EFFECTS OF A SMALL INTERVENTION CLASS

##### **Abstract**

Student achievement during the first two semesters at college is a predictor of the likelihood of attrition. In the following study, the causes of poor academic performance in the first semester are examined through interviews and questionnaires. A small intervention class is then implemented and administered to a random sample of students on academic probation after their first semester. The effects of this course on students' locus of control, academic self-efficacy, rate of retention, and GPA are measured. The course had a modest positive effect on retention and academic self-efficacy, but not on locus of control or GPA.

##### **Introduction**

I decided to expand my scholarship into the realm of human behavior change for two reasons. First was my desire to apply the same level of rigor to all of the aspects of my professional life. The goal of this self-imposed requirement is to elevate each part of my career to the high standards of evidence placed on the claims made in my research regarding the behavior of *mbuna* cichlids. Because of this standard, I hope to become a more capable and efficient educator, one of the pillars of my desired academic career path.

The second reason for undertaking an investigation of human learning was the satisfaction that comes with studying human behavior. The complimentary nature of the questions that I ask in human and in nonhuman systems satisfy a broader range of questions that pique my curiosity than would otherwise be possible. For example, I can ask questions regarding motivation in a way that is so far impossible to do with cichlids. On the other hand, some common themes arise between my two areas of research, which give me a unique advantage as I begin new investigations. For example, I use questionnaires and surveys to elicit responses from students and must determine if such instruments are indeed measuring the trait in question, which parallels the struggles I face when determining which proxies to use in order to measure female mate choice or male-male competition in cichlids.

Student attrition from colleges in the United States is a widespread phenomenon, where 21.3% of adults over 25, excluding those currently enrolled in a four year institution, have attained some college-level education, but not yet received a degree (U.S. Census Bureau, 2009). Attrition imposes real stresses on students and their families, as well as on universities. The financial cost to universities is the easiest to quantify, whereas costs to individuals and their families can only be estimated by comparing the income of individuals with different academic histories. Between 2003 and 2008, federal and state governments spent about \$9.1 billion on university appropriations and direct grants to students who did not return for a second year (American Institute of Research 2010). Though this sum does not take into account funds that universities received in tuition from these

students over the time of enrollment, one could argue that such funds should be added to the total amount of funding that society spends on college-level education that does not result in a college degree. Median annual income of adults who started but never completed a college degree is about \$31,054, which is about \$18,000 less than the income of adults who do have a degree from a four-year institution (\$49,303) (U.S. Census Bureau, 2009). For comparison, individuals who have completed high school but who have no other education earn an average of \$26,505 per year.

At the institution where the following study was conducted, a four-year, public university in the Northeast United States with over 30,000 undergraduate students, between 16 and 22% of first year students at one of the university's primary colleges are routinely asked to leave the university because of low academic achievement (Hills, personal communication).

Given that students who start a college education have academic skills at least strong enough to get into post-secondary institutions, it is reasonable to assume that the majority of these students have the potential ability to complete a degree. This is not to claim that such students should be given a degree upon acceptance to an institution, but rather that the ability to complete such a program is real, given the appropriate amount of individual effort and institutional support. Furthermore, it is imprudent to disregard struggling students who could be helped with minimal effort. Therefore, given the mutual self-interest of colleges and students, responsibility for finishing a college degree can and should be shared between these stakeholders.



Because of these issues, considerable effort has gone into studying the causes of student attrition, predicting those students who will struggle in their first semester at college, and minimizing the rate of attrition. Below is an overview of some of those efforts and techniques, as well as an assessment of their effectiveness.

### *Causes of student attrition*

A wide variety of factors have been identified that affect student retention. Known causes fall into roughly two categories: those that relate to an institution's climate, and those that stem from an individual's personal, cognitive or demographic background.

#### *Institutional factors*

Institutional variables include the college social environment and the degree to which a student feels integrated into it. Both the attitude towards the social environment and integration into that atmosphere are known predictors of attrition (Tinto, 1992; Allen *et al.*, 2008). Likewise, in a study that measured students' perceptions towards their institutions, Bean (1980) found that commitment to one's school accounted for the greatest amount of variation in the rate of attrition for both males and females. Interestingly, perceived quality of institution was positively correlated with retention for females, but not for males (Bean, 1980). Similarly, the students' feelings regarding being incorporated into the academic life of an institution have a moderately strong effect on persistence, at least for adult, non-traditional students (Sandler, 2000). Amongst a broader range of students, a) the degree to which they enjoy the physical university environment, b) feel like they

belong in the student community, and c) feel like university faculty and staff are sensitive to student needs, are highly predictive of students' intentions to remain enrolled in their institution (Willcoxson, 2010).

### *Personal factors*

Though the above-mentioned institutional factors affect retention, an individual's own achievement, personality, social support and self-esteem are also correlated with retention. For example, grade point average after students' first semester is, unsurprisingly, positively correlated with retention (Murtaugh *et al.*, 1999). Social factors are also known to affect decisions to remain enrolled in a four year academic program, especially loneliness and a lack of social support (Nicpon *et al.*, 2006). Monetary, familial obligations, and personal motivation to achieve are personal factors that affect retention (Christie *et al.*, 2004). Most of these factors cannot be affected by institutional support. However, educators should be aware of the effects that these variables have on student achievement. This will assist students with situations that, however personal, will affect their academic performance. For example, academic self-efficacy, which refers to "beliefs in one's capabilities to organize and execute the courses of action required to produce given attainments..." (Bandura, 1977), is known to be malleable in academic settings as students receive feedback on tasks (Bong & Skaalvik, 2003) and is positively correlated with retention (Zimmerman *et al.*, 1992; Chemers *et al.*, 2001).

Perhaps the broadest set of internal variables that have been shown to positively affect retention in a particular field of study relate to the student's ability to form coping strategies in the face of academic challenges. These include a)

confidence in acquiring content knowledge, b) persistence in sticking with challenging material, c) assertiveness, and d) the establishment of foreseeable long-term goals (Seymour & Hewitt, 1997).

One final personal factor affecting the likelihood of attrition is a student's locus of control, the extent to which one believes that causal actions reside in personal (internal) versus external forces (Rotter, 1954). A student's locus of control has long been known to correlate with academic success (McGhee & Crandall, 1968; Findley & Cooper, 1983). In other words, students who feel that they have control over the forces that affect their lives are more proficient than students who feel that they have relatively less control over such casual actions (McGhee & Crandall, 1968).

#### *Past efforts to minimize attrition*

A wide variety of techniques have been employed to mitigate student attrition in undergraduate institutions (Tinto, 1993). As expected, most of these interventions designed by institutions focus on institutional factors that affect retention, rather than internal student factors .

Blanc *et al.* (1983) showed that supplemental instruction attached to difficult, entry-level science courses have, in some cases, been shown to increase retention by 10% (67.3% to 77.4% reenrollment). Likewise, faculty-undergraduate research partnerships have been shown to have a similar effect on retention rates, decreasing attrition from 9.8% to 3.2%, although in a self-selected group of students (Nagda *et al.*, 1998). Randomized trials in which students were placed into different treatment

groups (either paired with faculty members to conduct research or placed in control group discussion sessions) show more equivocal results, where attrition was only significantly lower among African American students (10.1% versus 18.3%).

Other factors shown to affect undergraduate attrition include the quality of undergraduate advising by faculty members (Metzner, 1989) and orientation sessions (Pascarella *et al.*, 1986), both of which are thought to increase retention indirectly through increasing inter-personal social integration within the undergraduate population and by increasing their commitment to an institution. This is in addition to any direct benefit that high quality advising or orientation has on choosing the courses best suited to complete a degree within a desired time frame.

#### *Efforts to predict student attrition*

A variety of commercially and academically produced instruments have been developed with the purpose of predicting which first year students are likely to encounter academic challenges. Two such instruments are the Test of Reactions and Adaptation in College (TRAC) (Larose & Roy, 1995) and the MAP-Works® (Making Achievement Possible) system offered by Educational Benchmarking, Inc.

The TRAC instrument, developed to identify students who were likely to require additional institutional support to obtain a degree, measures “affective, cognitive, and behavioral dispositions” correlated with early college success (Larose & Roy, 1995). TRAC has been shown to add some predictive power beyond that offered by a suite of variables most often used to predict student success, such as

high school GPA and SAT scores, for some aspects of student success, such as hours studied per week and frequency of being late for class. It is, however, less able to account for much more variation than high school GPA and SAT scores in measures of actual success, such as GPA after the first semester (Lacrose *et al.*, 1998). Two subscales of the TRAC instrument were highly correlated with academic performance: Examination Preparation and the Giving Priority to Studies subscales (Lacrose *et al.*, 1998).

The MAP-Works® program is billed by its developer as “[identifying] students early in the term allowing for immediate support and intervention. MAP-Works® then serves as the infrastructure to manage those critical outreach efforts on your campus.” One major limitation in testing this product beyond the data provided by the manufacturer is that it is designed as a predictor and intervention tool in one package. Students who complete the web-based survey are immediately presented with a summary of their results and provided with strategies to improve weaknesses. The transition survey is designed to measure the following areas: a) academic skills and ability, b) learning, c) quality of course instruction, d) interference with class attendance, e) basic study skills, f) [advanced] study skills, g) self-management, e) self-efficacy, f) self-evaluation, g) encouragement and support, h) commitment to first year and to college, i) student interest [in campus activities], j) sense of belonging, k) on-campus living, l) homesickness, m) high school involvement, and n) an overall evaluation of adjustment to college life. Upon completion, students are categorized as being at high, medium, or low risk of attrition. Students at high and medium risk of attrition are immediately offered

coping strategies geared towards the student's areas of weakness. These include study tips, recommendations to see academic advisors or counselors, or lifestyle changes thought to increase academic performance.

### *Objectives of the Program*

I describe two studies below. Part I is a multi-faceted attempt to describe the causes of academic probation and to predict probationary status amongst students who had not been previously identified as "at-risk" through traditional means (primarily SAT scores and high school GPA). We conducted interviews with students on academic probation and with students in good academic standing in order to inform the creation of surveys. The aim of the surveys was to quantitatively differentiate students in these two populations in areas identified during the interview stage.

The second part uses the information gleaned from Part I to inform the creation of a small intervention course targeted to students who were on academic probation (GPA under 1.8 out of 4.0) after their first semester. We wanted to determine the ability of a small scale, targeted class intervention on variables known to affect student academic achievement and retention.

## **Methods: Part I**

### *Interviews*

In order to categorize students' self-perceived causes of academic probation, we conducted interviews with students who were on academic probation (GPA < 1.8 out of 4.0, n = 16) as well as students who were in good academic standing (GPA > 1.8, n = 21). We interviewed the group of students in good academic standing in order to compare differences in their perceptions of academic life and the perceived causes of academic difficulties between students who had achieved higher (>1.8) and lower (<1.8) GPAs. Interview questions (see Appendix A) were developed by Carron Chase, Rebecca Jordan, Steven Gray and David Mellor. Interviews occurred during April 2009. In order to maintain strict anonymity, answers to questions were recorded by interviewers by entering them into a word processor as the students reported their answers, in other words, no audio or visual recording equipment was used. In order to assure accurate recording of information, interviewees watched as their responses were recorded.

#### *MAP-Works®*

The MAP-Works® program was administered by university officials during the Fall of 2009 to all incoming undergraduate students. Response rates were over 90%, as resident assistants and orientation facilitators encouraged student participation.

### **Results: Part I**

#### *Interviews*

Interviews with students revealed a wide variety of issues facing incoming first year students. There were, however, few discernable differences between students who were on academic probation and those who were in good academic standing. For example, the initial response when asked: "What do you think has had the most negative influence on how you are doing in your classes at [this university]?" was roughly similar between groups in regards to blaming an external agent (high GPA: 54%; low GPA: 64%). Similar numbers of students had made at least a preliminary decision in regards to their major (high GPA: 95%; low GPA: 89%).

Though both groups of students reported meeting with an academic advisor during their first semester at roughly equal rates (high GPA: 73%; low GPA: 83%), students on academic probation were more likely to report negative reactions regarding their academic advising during their first semester than were students who were in good academic standing (low GPA: 13%; high GPA: 35%). Examples of negative interactions recounted by students on academic probation include inaccessibility and lack of response to student inquiries by advisors. This suggests that a) poor academic advising is a cause of low academic achievement or b) students who do poorly academically are more likely to report a negative interaction with their academic advisors.

When asked how they would change their university given complete control, both groups responded in a similar manner. Roughly equal proportions mentioned making classes easier (high GPA: 18%; low GPA: 12%), making substantive changes to the way courses are taught to encourage student engagement (high GPA: 23%;



low GPA: 24%), making classes smaller (high GPA: 18%; low GPA: 24%), or making a recommendation unrelated to academics (high GPA: 32%; low GPA: 35%) as their first response (e.g. dining, transportation, or housing).

Despite the lack of many discernable differences between the intervention and control groups, the interviews did reveal some notable insights. Most striking was a sense of “being lost” mentioned spontaneously by students on academic probation. This sentiment was not mentioned by any students in good academic standing. Such feelings hint at the psychological toll that poor academic performance can have on students, most of whom have done well up until their first semester at college.

#### *MAP-Works®*

There was no significant difference in GPA between students who were identified by MAP-Works® as being at high, medium or low risk (ANOVA:  $N = 670$ ,  $df = 2$ ,  $F = 2.11$ ,  $p = .122$ ) (figure 5.1).

## **Methods: Part II**

### *PASS course*

We developed the Portals to Academic Student Success (PASS) course based on information gathered during a literature review of issues surrounding attrition caused by poor academic standing, as well as interview and questionnaire-elicited experiences specific to students contacted through Part I. The syllabus was primarily developed by a single researcher, a faculty member at the study

institution, and focused on practical academic skills, notably: note-taking, effective study techniques, stress management, short term (semester), medium term (less than five years) and long term (greater than five years) goal setting and a four-year academic plan. In addition to assignments directly related to the previous topics, students wrote essays reflecting on the causes of their probationary status and, at the end of the course, the changes necessary in order to maintain a GPA over 1.8.

We addressed topics beyond just academic skill sets. This was necessary because of the information gathered from interview data concerning the methods of instruction in undergraduate classrooms (see Results, Part I). Specifically, we included content recommended by Bransford *et al.* (1999). This included the promotion of metacognitive reflection, self-assessment, and community strengthening. In addition, the negative interactions with academic advisors mentioned by students on academic probation suggested the need for small class sizes where informal advising could occur with knowledgeable instructors and where students could be assisted in the development of a four-year academic plan.

Furthermore, in order to enhance the transfer of concepts from the PASS course to other situations, the goals of every lesson and the nature of the problems identified during each class were made explicit to the students (Halpern, 1998). Transferring ideas refers to applying ideas and knowledge from the instructional context to another context (Barnett & Ceci, 2002). The unique historical identity of the institution as an agricultural-themed college environment in a densely-populated urban and suburban area has created an institutional identity that should be conducive to community-based education. Such a community organization

should be able to create the type of learning environment in which educational gains have been shown occur (Colby *et al.*, 2003).

Forty-eight students of the 127 who earned GPAs below 1.8 in the Fall of 2009 were randomly assigned one of the six instructors. Before the first day of class, five students were removed from the class because of unresolvable scheduling conflicts, leaving 43 students enrolled. Classes met for 80 minutes, once per week for ten consecutive weeks during the students' second semester in college, except for one week during the mid-semester break.

Peer and self-assessment were used to measure the effectiveness of academic skills and self-reflective essays. The rubrics used for assessment were created during student-faculty discussion, but guided towards assessments created for scientific content knowledge described in Etkina *et al.* (2006), and those developed for inquiry-based units (Diamond, 1998; Schunn *et al.*, 2004). The use of student-generated formative assessment has been shown to increase scientific content knowledge and transfer (Etkina *et al.*, 2006), and it was expected that this would be true for other realms of knowledge.

A goal of creating this course was to generate a single learning environment that merges academic, civic, and social endeavors. While social theorists have long argued that learning is a social enterprise, the university classroom is not structured to engage students in multiple cognitive realms. Indeed educational discussions at scientific meetings (Jordan pers. comm.) reveal that many scientists are reluctant to engage their students socially and civically because of lack of expertise on the part of faculty members and because of a fear of losing rigor in the science classroom.

### *Locus of Control*

We measured the degree to which students possessed an internal or external locus of control a total of four times for three different groups: 1) Students enrolled in the PASS course at the beginning of the semester, 2) students enrolled in the PASS course at the end of the semester, 3) students with a GPA from their first semester of less than 1.8 and 4) students with a GPA from their first semester that was greater than 1.8. The Internal Control Index (Dutteiler, 2002) was used to measure the locus of students' control. This measure employed a ranking scale for each question in the validated instrument. PASS students (groups 1 and 2) filled out surveys during class time, while students from groups 3 and 4 were contacted through e-mail and given \$15 to come to a classroom at a time of their choosing to complete the instrument.

The non-parametric, Kruskal-Wallis ANOVA was used to compare the LOC rankings of each population. Mann-Whitney U tests were used to test for post-hoc comparisons between each group if the Kruskal-Wallis test suggested that differences existed.

### *Academic Self-Efficacy*

Students' self-efficacy in regards to academic aptitude was measured with a validated instrument developed by Owen and Froman (1988). The instrument was given at the same time as the locus of control questionnaire and to the same

populations (see above). As with LOC measurements, a Kruskal-Wallis ANOVA was used to compare populations with Mann-Whitney U test for post-hoc comparison.

Discriminant function analysis was employed to determine which questions explained the greatest amount of variation between the following groups of students: 1) academic probation pre PASS v. academic probation post PASS v. academic probation no PASS v. students in good academic standing and 2) academic probation pre PASS v. academic probation post PASS and 3) academic probation pre PASS and academic probation non PASS v. students in good academic standing.

#### *GPA and Retention*

Grade point averages at the end of the 2nd and 3rd semesters were used to compare the two groups of students who earned a 1st semester GPA < 1.8. The first (PASS) group was enrolled in the PASS class during their 2nd semester and the second (non-PASS) group was not enrolled in PASS. Retention was likewise compared at the end of students' second and third semesters after initial enrollment at college. The number of students remaining enrolled into their third semester was compared between the PASS and non-PASS populations, and a Mann-Whitney U test was used to compare the GPAs of PASS and non-PASS students who remained enrolled.

## **Results: Part II**

### *Locus of Control*

There were significant differences in the locus of control scores between the four comparison groups (students in good standing, probation students pre-PASS, post-PASS, and non-PASS) (Kruskal-Wallis ANOVA;  $N = 120$ ;  $H = 9.41$ ;  $df = 3$ ;  $p = 0.024$ ). Post-hoc analysis reveals that the locus of control of students who were in good academic standing was significantly more internal than the combined population of students who earned low GPAs (the non-PASS students and the pre-PASS students who were enrolled) (Mann-Whitney U Test;  $N = 36, 45$ ;  $Z = 2.30$ ,  $p = 0.022$ )(figure 5.2). Interestingly, once enrolled in the PASS course, students' LOC did not change significantly, and the trend ran counter to the expected direction (i.e. toward a more external locus of control) (Mann-Whitney U Test;  $N = 32, 13$ ;  $Z = 1.83$ ,  $p = 0.068$ ) (figure 5.3).

#### *Academic Self-Efficacy*

There was a significant difference in students' academic self-efficacy among the four comparison groups (students in good standing, probation students pre-PASS, post-PASS, and non-PASS) (Kruskal-Wallis ANOVA;  $N = 120$ ;  $H = 10.19$ ;  $df = 3$ ;  $p = 0.017$ ). Post-hoc analysis revealed that after participating in the PASS course, PASS students reported a higher academic self-efficacy than AP students not enrolled in PASS (Mann-Whitney U Test;  $N = 39, 13$ ;  $Z = 2.64$ ,  $p = 0.008$ ). Furthermore, the combined scores of students with a low GPA but not enrolled in PASS and the students enrolled in PASS before taking the course were significantly lower than students with a high GPA (Mann-Whitney U Test;  $N = 45, 36$ ;  $Z = 2.43$ ;  $p = 0.015$ ) (figure 5.4). After participating in the PASS course, students reported a

higher academic self-efficacy, but not significantly so (Mann-Whitney U Test;  $N = 32$ ,  $39$ ;  $Z = 1.77$ ;  $p = 0.077$ ). We did not find any other significant differences (figure 5.5).

The results of the discriminant function analysis show that the following five questions weighted highest to maximize the differences between the four groups of students (AP pre PASS, AP post PASS, AP non-PASS, and non-AP), ranked from highest to lowest. "I (student) am confident in my ability to...

- 1) Apply lecture content to lab
- 2) Understand difficult passages in texts
- 3) Understand ideas in class
- 4) Ask questions in a large classroom
- 5) Listen carefully during a hard lecture"

The following five questions weighted lowest in discriminating between the four groups, listed with the question with the lowest ranking first. "I (student) am confident in my ability to...

- 1) to earn good grades
- 2) to use a computer
- 3) to master content in a course in which I am not interested
- 4) to challenge a professor's opinion in class
- 5) to participate in extracurricular activities "

The discriminant function analysis was able predict student placement into their category (AP pre PASS, AP post PASS, AP no PASS and non AP) 67% of the time. Based on a proportional chance criteria of correctly assigning group membership 25% of the time using random allocation, this measure of academic self efficacy

appears to be a reliable method of grouping students based on academic achievement and intervention assignment.

The following five questions weighted highest in maximizing the differences between students on AP before the PASS course compared to students at the end of the PASS course. “I (student) am confident in my ability to...

- 1) to tutor another student
- 2) to master content in a course in which I am not interested
- 3) to understand difficult passages in texts
- 4) to earn good grades
- 5) to use the library”

The discriminant function analysis was able to predict student placement into their correct category (pre PASS versus post PASS) 83% of the time. Based on a proportional chance criteria of correctly assigning group membership 50% of the time using random allocation, this measure of academic self efficacy appears to be a reliable method of grouping students based on the PASS intervention.

The following five questions weighted highest in maximizing the differences between students who were on AP at the beginning of the semester (AP pre PASS and AP non PASS) versus those were always in good academic standing (non AP). “I (student) am confident in my ability to...

- 1) take essay tests
- 2) understand difficult passages in texts
- 3) apply lecture content to lab
- 4) understand ideas in textbooks



5) take well organized notes”

The following five questions weighted lowest in maximizing the differences between students who were on AP at the beginning of the semester (AP pre PASS and AP non PASS) versus those were always in good academic standing (non AP). “I (student) am confident in my ability to...

- 1) ask a professor to review material
- 2) take objective tests
- 3) master content in a course in which I am not interested
- 4) spread out studying instead of cramming
- 5) use a computer”

The discriminant function analysis was able to predict student placement into their correct category (AP pre PASS and AP non PASS versus non AP) 77.6% of the time. Based on a proportional chance criteria of correctly assigning group membership 50% of the time using random allocation, this measure of academic self efficacy appears to be a reliable method of grouping students based on academic achievement.

### *GPA*

By the end of the students’ first full semester after taking part in the PASS course, their third semester at college, there was no significant difference in cumulative or term GPA among students who had been enrolled in the PASS course and those students who earned less than a 1.8 GPA in their first semester but had

not been enrolled in the PASS course (Mann-Whitney U: 3<sup>rd</sup> term GPA:  $N = 54, 32, Z = .78, p = .43$ ; cumulative GPA:  $N = 54, 32, Z = .83, p = .41$ ).

### *Retention*

Of the 84 non-PASS students who earned a GPA below 1.8 in their first semester at college, 54 were still enrolled by the end of their third semester. This translates to a 35.7% rate of attrition in the absence of intervention. Of the 43 students who participated in the PASS course, 32 were still enrolled by the end of their third semester (25.6% attrition rate) (Figures 5.6 and 5.7).

### **Discussion**

The most striking result from this small class intervention is the effect it has had on the rate of retention. The 10% lower attrition rate among the students in the PASS course suggests that small-scale interventions can mitigate attrition amongst students who later prove an ability to continue matriculating.

Interestingly, after completing the PASS course, students' self-perceived sense of academic self-efficacy was significantly higher than students who were on academic probation but not enrolled in PASS, despite the fact that there was no difference in GPA between these two groups. One possible explanation for this phenomenon is a boost in self-esteem that does not coincide with an actual increase in academic ability, yet is sufficient to affect the retention rate among students who are not forced to withdraw because of GPA requirements. The disconnect between individuals' perceived and actual aptitude has been described previously as the

Dunning-Kruger effect, in which individuals are unable to accurately assess their own abilities because of their lack of the knowledge required to actually possess mastery of a subject or ability (Kruger & Dunning, 1999).

The failure of MAP-Works® to accurately predict student achievement may be the result of two effects. First, MAP-Works® was designed as an intervention tool. If at-risk students are told early on that they are likely to perform poorly in the coming semester, it is possible that this information alone can prompt them to better self-regulate. In other words, the warning may spur metacognitive awareness that leads to an increase in self-regulated learning activities. Boekaerts and Corno (2005), reviewed the use of classroom interventions designed to increase self-regulation, though, to our knowledge, the use of a self-regulation assessment tool itself as an actual intervention has not been studied in first-year university settings. Alternatively, the fact that the MAP-works pre test results are reported to the students could have a priming effect on the receiver: making the student more likely to achieve at the predicted level than they would have otherwise been.

Though the average locus of control measure did not change over the course of the semester, this was not entirely unexpected. The evidence suggests that locus of control can change in individuals over decades in regards to some specific domains (Lachman, 1986), whereas short term change has typically required intense, in-patient psychiatric treatment (Roberts *et al.*, 1992).

Students on academic probation reported more negative interactions with advisors than students in good standing. It is possible that poor advising caused a certain degree of academic troubles in the first semester, though it seems equally

plausible that, in retrospect, students who wish they had been advised to take an easier course load are the ones likely to report negative advising experiences. It is also possible that students with a more external locus of control, who are known to be at higher risk of academic troubles, are more likely to blame an external agent than those student with a more internal locus of control.

### *Future Directions*

Though successful in affecting the rate of retention among students on academic probation, other goals remain elusive. Given the difficulties in affecting student achievement in a small-scale, short-term intervention, it is perhaps wise to broaden the scope of the intervention. Because of the legacy that the focus school has in the natural sciences, it may benefit from using a program that others have successfully implemented, the Environment as an Integrating Context (EIC). In this model, multiple courses are taught around a unifying, local environmental question. Courses are typically multidisciplinary, team-taught, and demand problem-based learning goals (Lieberman & Hoody, 1998). Furthermore, by focusing on local environmental issues, EIC can increase students' sense of community, known to positively affect retention (Tinto, 1992).

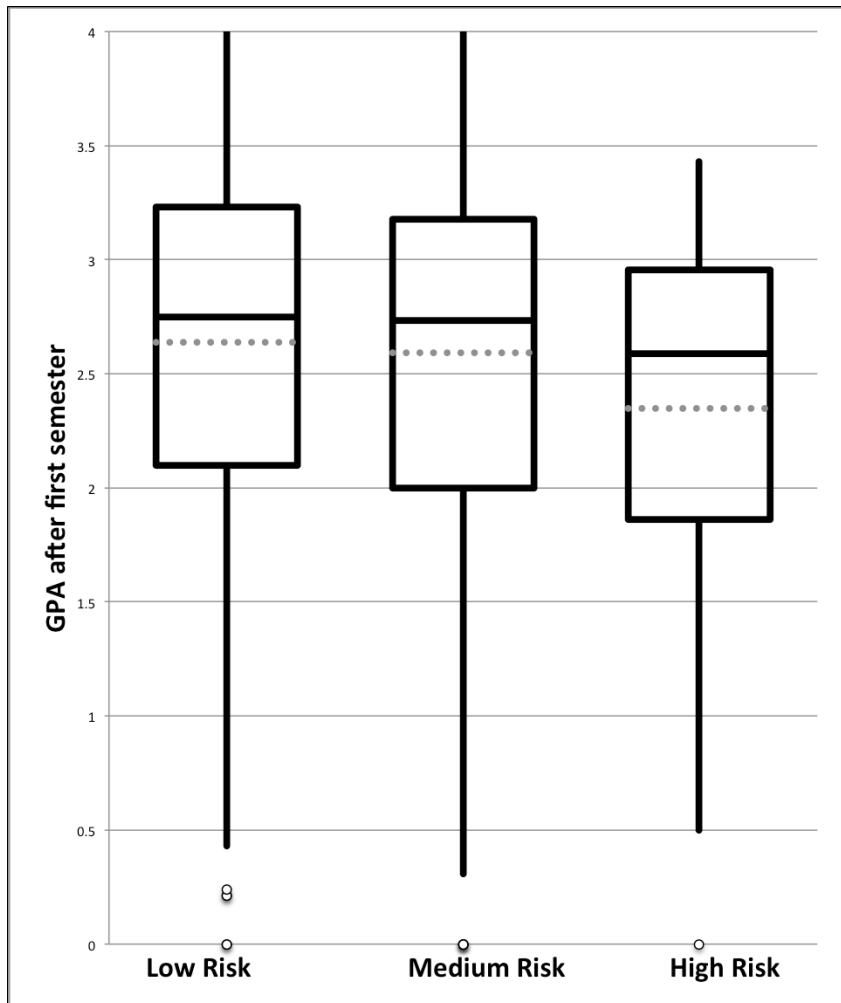


Figure 5.1. GPA of students categorized by MAP-Works risk group. Whiskers represent the upper (75%) and lower (25%) quartiles, boxes the middle (50%) quartile, and outliers are determined by exceeding the 9<sup>th</sup> or 91<sup>st</sup> percentiles, though they were used in the analysis. Median response is represented by the solid line in the box. Dashed lines show sample means.

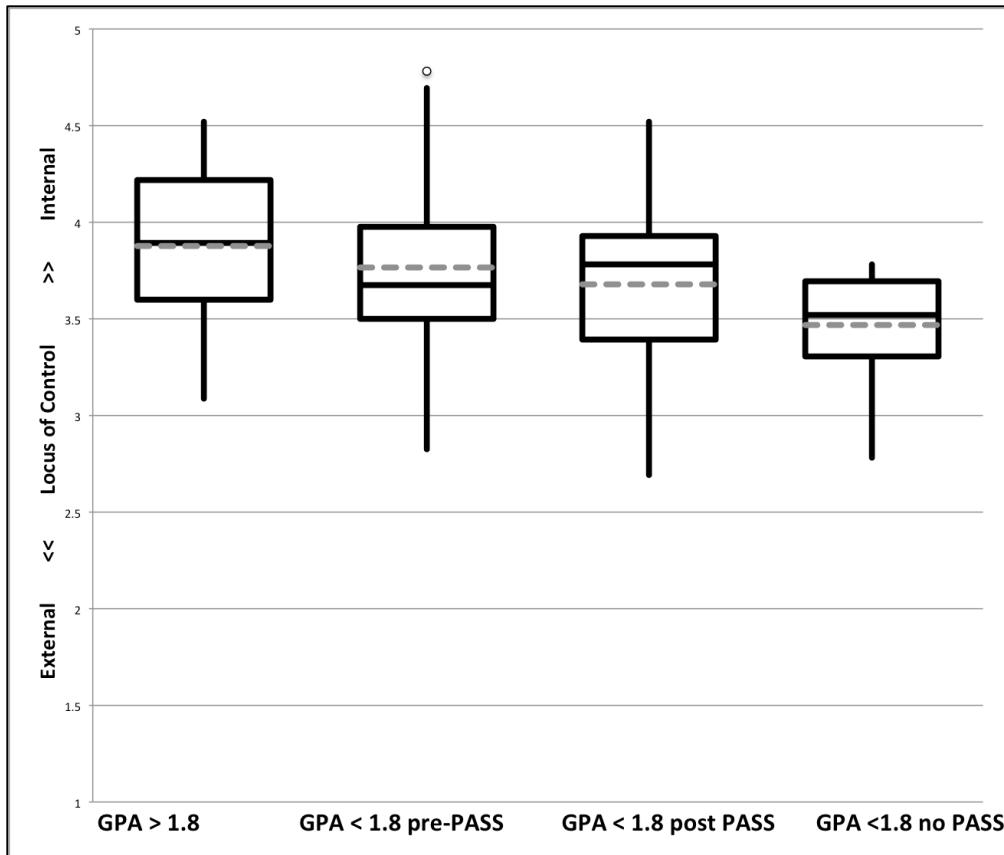


Figure 5.2. Students' locus of control based on academic performance. LOC was measured in students enrolled in PASS at the beginning and end of the course. Whiskers represent the upper (75%) and lower (25%) quartiles, boxes the middle (50%) quartile, and outliers are determined by exceeding the 9<sup>th</sup> or 91<sup>st</sup> percentiles, though they were used in the analysis. Median response is represented by the solid line in the box. Dashed lines show sample means.

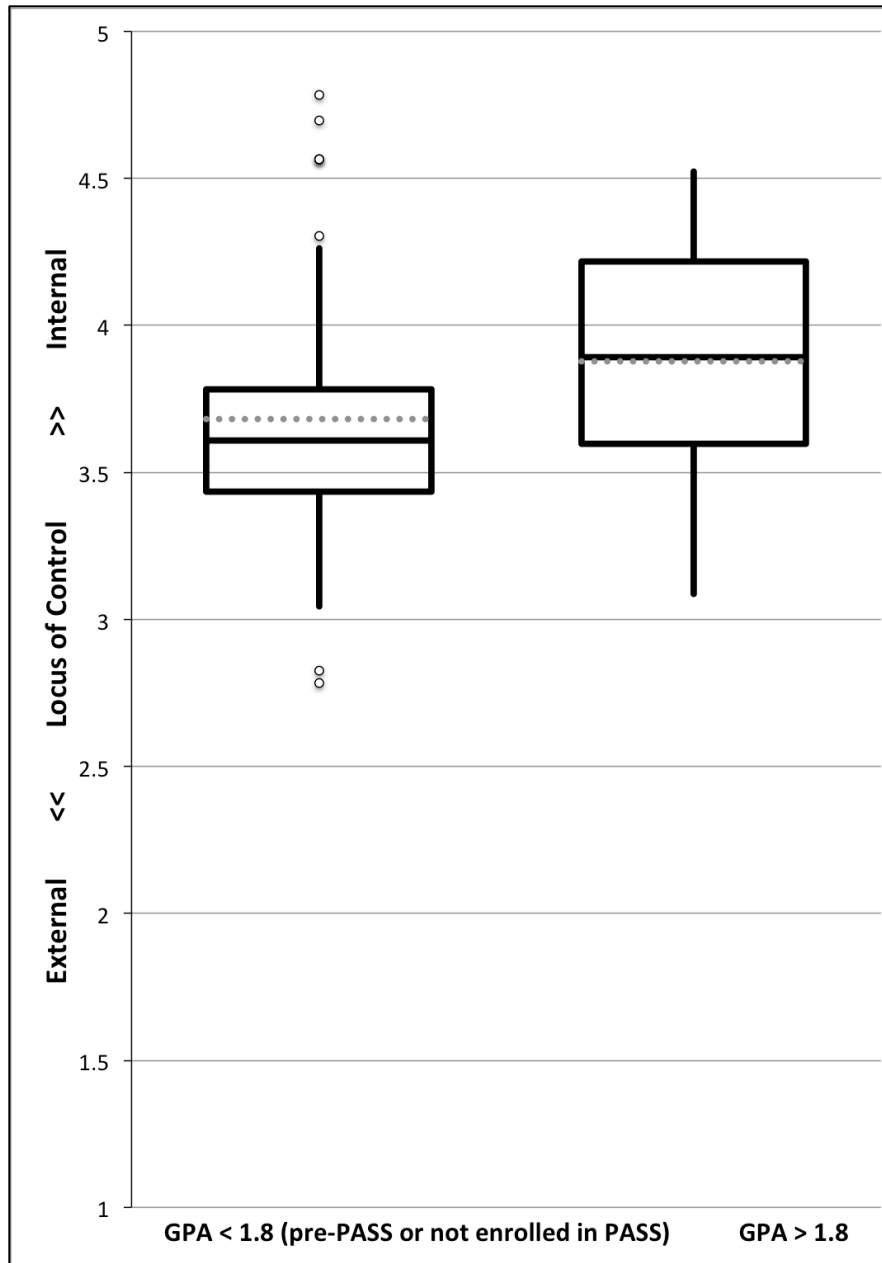


Figure 5.3. Locus of control of students on academic probation, regardless of PASS enrollment, and LOC of students in good academic standing. Whiskers represent the upper (75%) and lower (25%) quartiles, boxes the middle (50%) quartile, and outliers are determined by exceeding the 9<sup>th</sup> or 91<sup>st</sup> percentiles, though they were used in the analysis. Median response is represented by the solid line in the box. Dashed lines show sample means.

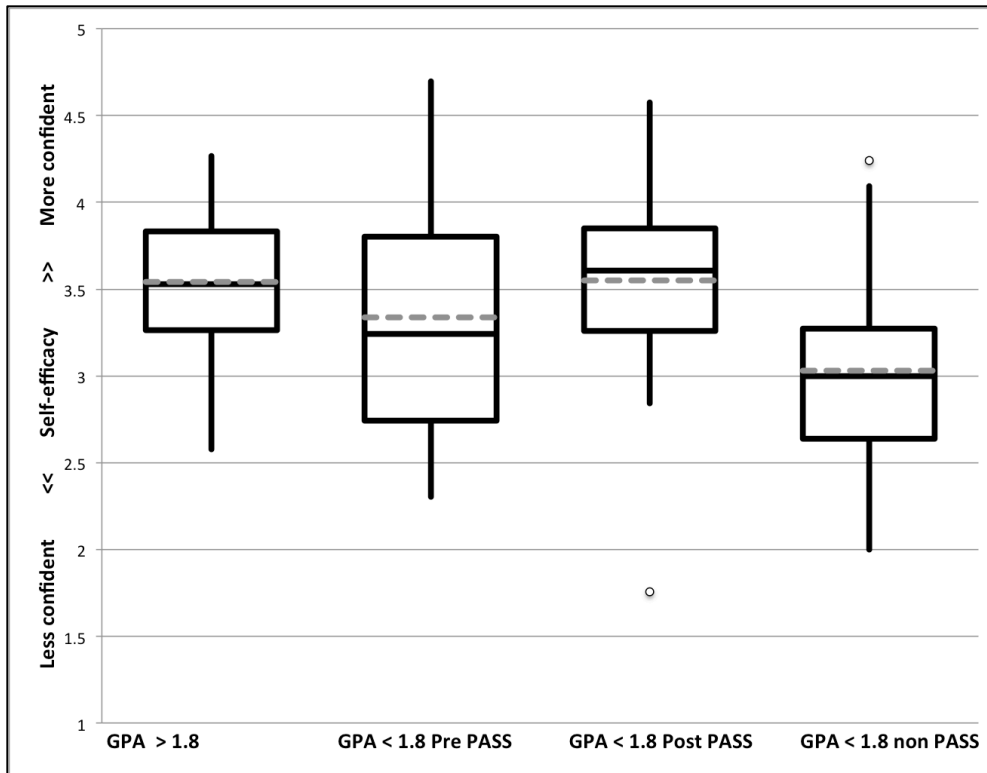


Figure 5.4. Academic self efficacy of students in good academic standing, poor standing before the PASS course, after the PASS course, and students in poor standing not in the PASS course near the end of their second semester. Whiskers represent the upper (75%) and lower (25%) quartiles, boxes the middle (50%) quartile, and outliers are determined by exceeding the 9<sup>th</sup> or 91<sup>st</sup> percentiles, though they were used in the analysis. Median response is represented by the solid line in the box. Dashed lines show sample means.



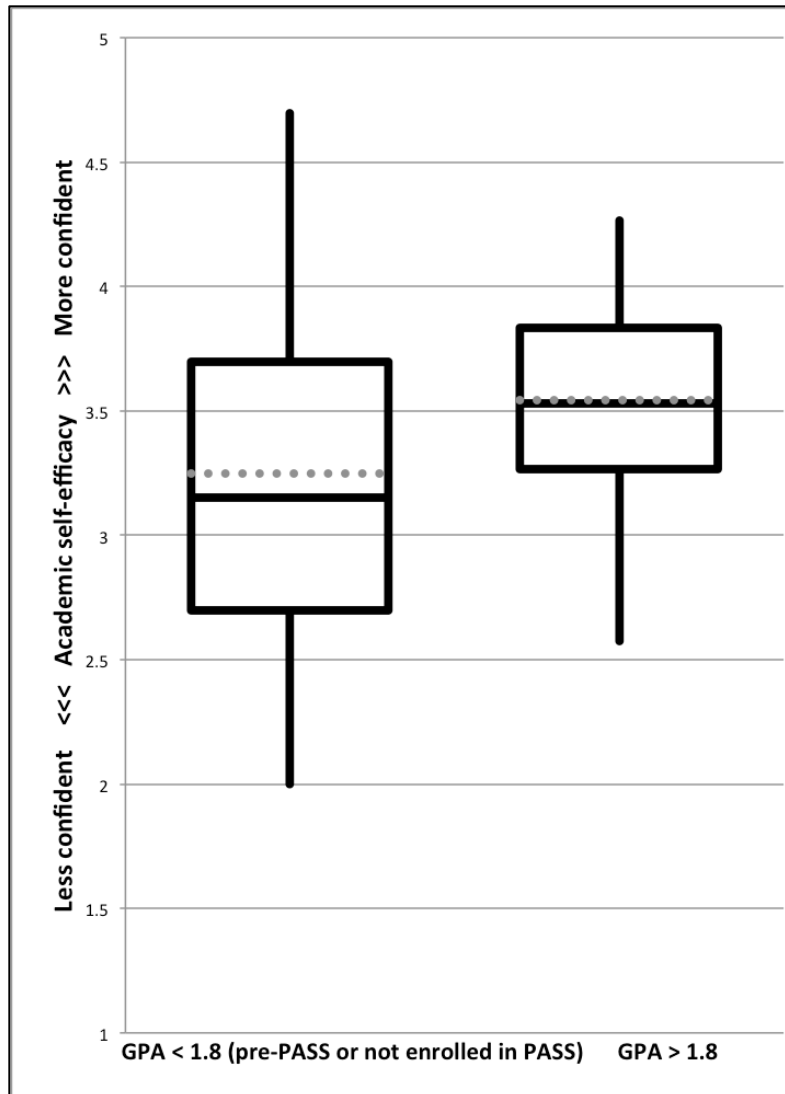


Figure 5.5. Academic self efficacy of students in poor academic standing, regardless of PASS enrollment, and in good academic standing. Whiskers represent the upper (75%) and lower (25%) quartiles, boxes the middle (50%) quartile, and outliers are determined by exceeding the 9<sup>th</sup> or 91<sup>st</sup> percentiles, though they were used in the analysis. Median response is represented by the solid line in the box. Dashed lines show sample means.

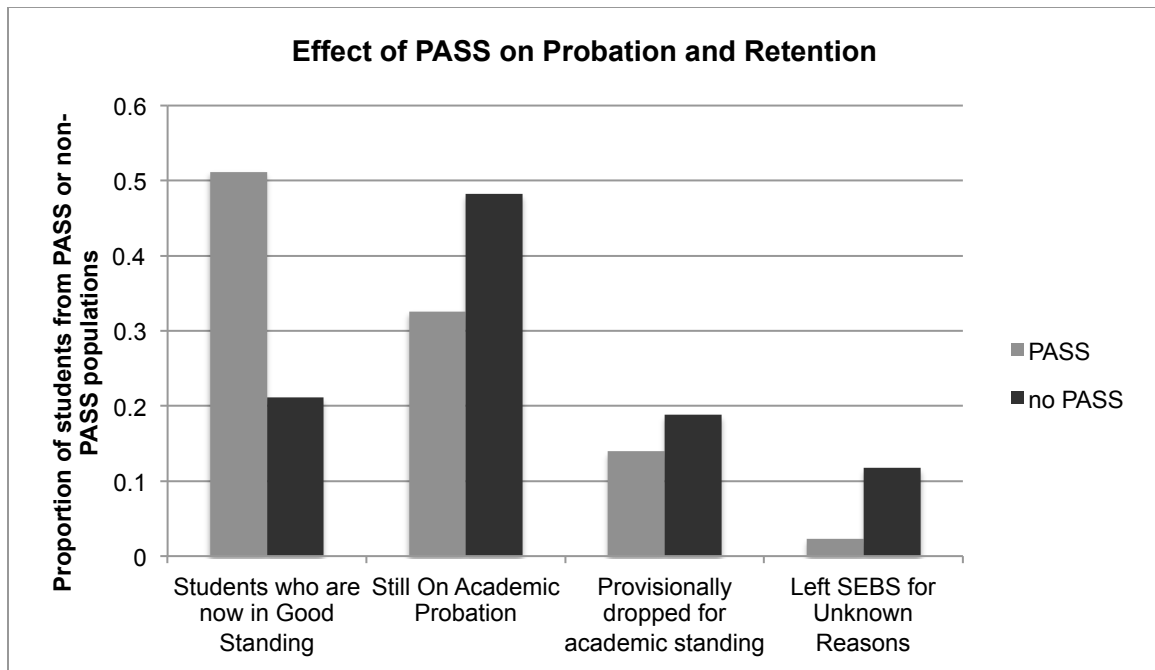


Figure 5.6: Comparison of students enrolled in the PASS course or not at the end of their second semester who were in poor academic standing at the end of the second semester. "SEBS" refers to the Rutgers University School of Environmental and Biological Sciences.

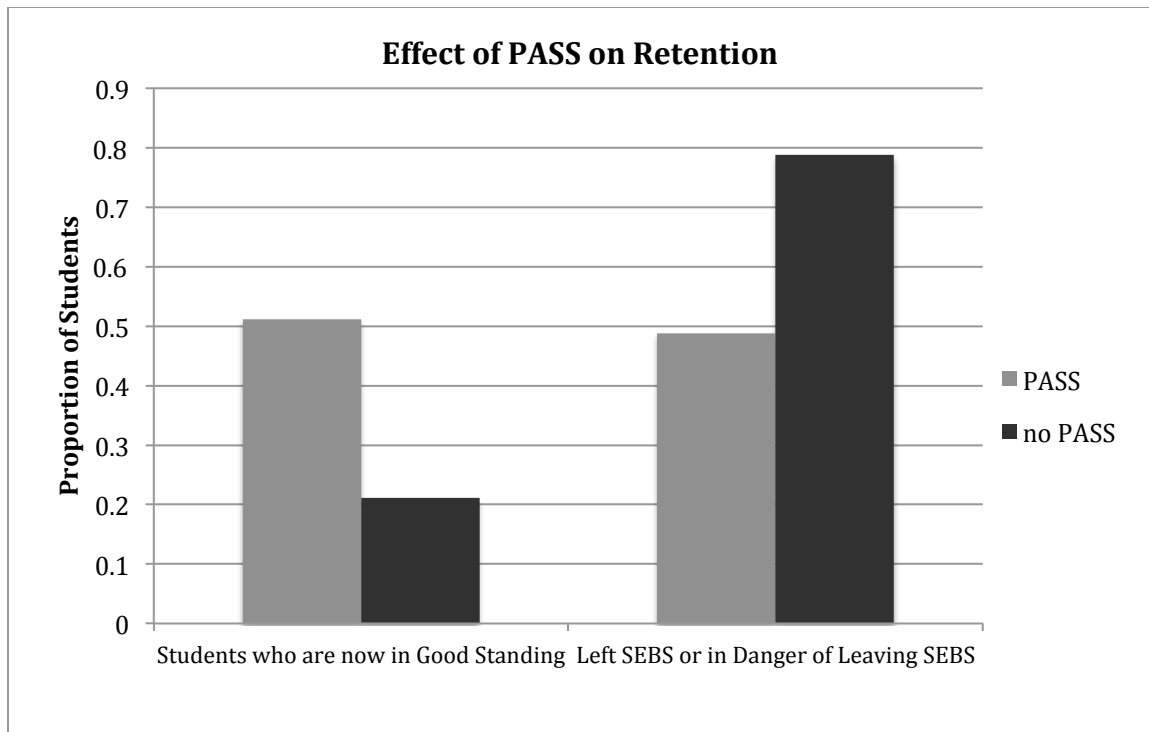


Figure 5.7. Comparison of students at the end of their second semester based on PASS enrollment. The second category ("Left College or in Danger of Leaving College") lumps together students in the second, third, and fourth categories of figure 6).

## Appendix A, Questions asked to Students During Interviews

(1) What is your major?

(2) What are some things you like about [this university]?

[follow up] What class have you taken that you have enjoyed at [this university]?

(3) What are some things you don't like about [this university]?

[follow up] What class have you taken that you have not enjoyed at [this university]?

(4) Are there certain courses that are giving you particular trouble?

(5) About how many hours per day do spend studying outside of class? 0, 1-2, 3-5, 6 or more?

(6) Have you ever taken, or heard about, a class that was designed to "weed out" students?

[follow up] What class was it?

[follow up] What made it a 'weeding out' class?

(7) Do you have to take "weed-out" classes like that in the future? Do you think you will do well?

[follow up] Why do you think you will do well (or) not well?

[follow up] Do you think these classes should be changed? If so, how?

(8) What do you think has had the most positive influence on how you are doing in your classes at [this university]?

[follow up] Why do you think that these things affect your grades?

(9) What do you think has had the most negative influence on how you are doing in your classes at [this university]?

[follow up] Why do you think that these things affect your grade?

(10) Is [this university] more or less like what you thought it was going to be before you came here?

[prompt] If no – what is different?

[prompt] If yes- what were your expectations?

(11) Do you feel that your high school experiences prepared you for your first year at [college]? Please explain.

We are trying figure out how well or not well, some students transition from high school to Rutgers.

[prompt] How about socially?

[prompt] How about academically?

(12) What advice would you give your high school about preparing students to do well at [this university]?

(13) If a friend of yours was coming to [this university], what advice would you give them about student life and acclimating to Rutgers?

[follow up] What about advice regarding doing well in classes?

\*(14) When you think about students other than yourself who find themselves on academic probation, why do you think that happens?

\*(15) What would you recommend the university do to help those students succeed?

\*(16) Why do you think you are on academic probation?

\*(17) What happened when you learned you were on academic probation? Did you talk to anyone about your academic status? How did they react? Who would you talk to? Explain: E.g. Are your parents or anyone else concerned about your grades at [this university]?

\*(18) Are you worried about your academic status? Do you think you will improve and why?

\*(19) How important is it for you to get off of AP?

(20) Do you feel that your instructors (like professors or TAs) or any other employees of Rutgers are concerned about your grades? [follow up] Why or why not?

(21) Have you been in contact with your academic advisor?

[follow up] If no .. why not?

[follow up] If yes ..

[follow up] A. What are some good things about your advisor?

[follow up] B. What are some bad things about your advisor?

(22) What do you think would help you improve your GPA?

(23) If a friend were coming to RU, what advice would you give? What about advice about staying off probation?

(24) If you had complete control and could change anything about [this college or university], what would you change?

(25) Did anything about student life surprise you when you got here?

(26) Other than being in class or studying what do you spend the rest of your time doing on a typical day?

(27) Rutgers has a reputation as a party school. How often do you see people getting carried away with that and losing track of their coursework?

[follow up] What about you? How do you try to balance that?

[follow up] Is that working for you?

(28) Are your parents concerned about your academic performance.

[follow up] Why or why not?

(29) Where do you live?

[follow up] On campus? Where?

[follow up] Off campus? Where?

(30) In what types of extra curricular activities are you involved? Are you involved in any student clubs? What do you do for fun? Have you found it easy to make new friends at Rutgers?

(31) Do you have a job? If so, where and how often?

(32) Do you have anything else you would like to share about things we have discussed?

## Appendx B: Syllabus for Portals to Academic Student Success

### **Portals to Academic Study Success (PASS) (1 credits)**

**11:015:103**

#### **Description:**

The purpose of PASS is to engage students in learning about the processes by which individuals learn in class and, ultimately, achieve academic success. The course is geared to freshmen probationary students in a semi-individualized, small discussion/seminar format. Topics include time management, developing successful study habits, long-term goal planning, and use of university-wide resources.

#### **Course goals:**

- 1) Implement appropriate class attendance and note-taking skills.
- 2) Develop learning strategies.
- 3) Develop time and stress management skills.
- 4) Develop an individualized 4-year study plan towards graduation.
- 5) Understand how learning occurs with specific reference to each individual student.

#### **Grading:**

Attendance (5 points x 10)	50*
Homework (10 points x 6)	60
<u>Participation</u>	<u>30</u>
	140

\*Attendance is mandatory.

**Portals to Academic Study Success (PASS)  
Syllabus Spring 2011**

<b>Lecture</b>	<b>Topic</b>	<b>Homework</b>
1	Introduction/Purpose Pre-assessment	What “happened” last semester to cause you to end up on probation?
2	Personal responsibility I: Professionalism Organization Time Management <b>Video: Strategic Learning &amp; Time Management</b>	Diagram a pie chart of activity in one day.
3	Personal responsibility II: Organization Note-taking <b>Video: Note-taking</b>	Set up a weekly plan with blocked activities. Example of notes taken in class/re-writing of notes.
4	Study Habits	
5	Goal setting	4 year plan (Anticipated major, all courses for the next 3 years, graduation date, financial plan)
6	(Based on needs of students)	
7	(Based on needs of students)	
8	Teaching Presentation	Each student will “teach” a topic from one of their classes
9	Teaching Presentation	What changes have you made this semester? What worked and didn’t work?
10	Final Plan I Post-assessment survey	



## Teaching points

### Lecture 1: Purpose of course

- introduce yourself and get familiar with each other, go over syllabus
- difference between high school and university
- to help understand how to succeed in classes at Rutgers (class attendance, etc)
- talk about how each of them ended on probation
- changes in behavior that will lead to success in class
- What is success?
- Learning and success is highly individualized (there is no ONE answer/method)
- What kind of contact have they had with faculty, TAs, advisors, counselors, RAs, etc?
- (depending on the availability of Internet in room, either assign a video or show the video in Lecture 2)

### Lecture 2:

- Show video on Strategic Learning and Time Management
- Discuss importance of class attendance, keeping up with homework, readings
- Personal responsibility, Procrastination- how to manage self-motivation, divide work into manageable sizes, work on something else when you are stuck, etc.
- How much time should you be spending on each course (2 hours outside of class/1 contact hour)
- Making contact with TAs, professors, study groups, MSLC informatio
- GPA calculator
- (Assign Note-taking video)
- 

### Lecture 3:

- Show Note-taking video and discuss what taking notes mean, re-reading or re-writing notes after each class
- Figuring what the professor wants in each class, type of exams etc.
- Time management- how you spend your week, plus looking forward to the entire semester which means putting all homework, papers due, midterm and final exam dates and time on calendar
- Study/work/read in small manageable size pieces throughout semester instead of cramming
- Work through example of an entire week 128 hours: hours in class, on bus, eating, sleeping etc.

### Lecture 4: How to Study?

- People learn: visual, auditory, repetition, memorization
- Active review, practice tests, retrieval of information
- Everybody is different, need to figure out how it works for you
- Recent study show changing study location improves retention, varying the type of material studied in a single sitting leaves deeper impression on brain and studying slowly throughout semester (called spacing) improves recall vs. cramming

### Lecture 5: Goal setting

- How to declare a major? How to decide what major to pick?

- Important webpages: Online schedule of classes, Degree Navigator, SEBS/SAS graduation requirements, various Departmental homepages
- Importance of knowing what you need to graduate, course planning, Study abroad, senior honors project
- Don't just think one class at a time

#### Lecture 6 & 7

- Based on student-identified needs

#### Lecture 8 & 9: Teaching presentation

- Concept that you only truly learn a subject when you have to teach it
- Divide class and ask each to teach a topic you are currently learning

#### Lecture 10: Summing up

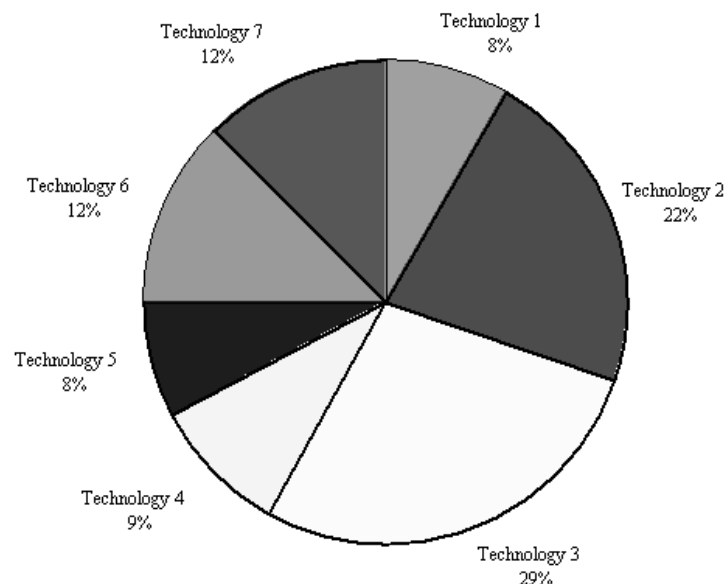
#### Rubric for homework assignments

##### **Assignment 1: Short essay on what "happened" last semester.**

10 points: A readable thoughtful essay. It should be clear that the student put effort/time into the composition.

##### **Assignment 2: Pie chart of daily activity.**

10 points: A neat pie chart diagram, plus a list of the categories. Diagram should reflect the % of time in each activity. May be produced by Excel or hand-drawn. Evidence of time and effort spent in preparing the diagram. In addition, students are expected to be able to explain their chart during class discussion (part of learning communication skills).



**Assignment 3: Weekly planner of classes and activities (study, library, tutoring, etc).**  
**(This activity may proceed for several weeks.)**

5 points: Again, clear evidence of effort put into homework is required. Clear explanation of chart.

eg.

	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
8:00am							
9:00am			Lecture				
10:00am	Lecture		Lecture	Lecture		Sport	
11:00am	Lecture	Lecture				Sport	
12:00am			Library		Lecture	Sport	
1:00pm		Library	Study			Sport	Study
2:00pm	Lecture	Study	Study	Lecture		Sport	Study
3:00pm	Lecture	Study		Lecture		Sport	Study
4:00pm					Lecture	Sport	Study
5:00pm			Lecture				
6:00pm			Training				
7:00pm	Study	Study	Training	Study	Study		
8:00pm	Study	Study		Study	Study		

5 points: Example of lecture notes showing re-writing or editing/highlighting or writing out important vocabulary words onto index cards.

**Assignment 4: 4 year plan towards graduation.**

10 points: List all courses in 8 semesters (or more) towards a specific major. Should be listed by semesters. Core courses and electives should be highlighted in different colors. This will require the students utilize Degree Navigator software and to figure out the various SEBS requirements, SEBS major requirements and general elective choices.

**Assignment 5: Class presentation**

10 points: Each student will present a topic that they are currently learning in a class. Each presentation should be about 15 minutes long.

**Assignment 6: Final essay on what changes they have made this semester.**

10 points: The essay should address what study skills/time management/organization/note-taking/stress management issues they have learned, and what “worked” and what didn’t work for them.

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## CONCLUSIONS

My work will inform the field of behavioral ecology through three primary avenues. The first significant endeavor is my focus on intraspecific behavioral processes over interspecific ones. The reason these trials are necessary is that only by investigating these interactions can we find support for or against sympatric differentiation leading to eventual speciation. The emerging narrative surrounding the radiation of this spectacular lineage relies heavily on sexual selection for enhancing the rate of diversification. However, the evidence so far only suggests that sexual selection, both male-male interactions and female mate choice, reinforce the differences that arise in allopatry. Though this has been demonstrated many times, it does not rule out differentiation occurring in sympatry. My work is the necessary first step to demonstrate that these process can happen in sympatry. For example, the fact that female preference is affected by the outcomes of male-male contest interactions, suggests that females distinguish between conspecific males, which has only been demonstrated in a few other groups, and is usually only conclusively seen in interspecific trials where females show preference for conspecifics over heterospecific males or similarly color heterospecifics over differently colored heterospecific males.

The second major contribution that I have added to the field is to further the investigation of male behavior in the life history of this diverse model system. Until recently, the only evidence that sexual selection affected the diversity of this group of fishes was the evidence gathered from observations of male nuptial color

distribution. My behavioral studies show that male-male interactions affect female preference and that these effects are consistent with the types of behaviors that are expected if these fish diversify through sympatric speciation driven by sexual selection. I have also determined the threshold at which males distinguish between conspecific rivals. This sensitivity has not been demonstrated previously and, as above, is necessary, though insufficient, to demonstrate that behavioral interactions can result in disruptive selection leading to sympatric speciation. These color-mediated interactions suggest that males are focusing their aggression on those males that pose the most acute competition to their territory establishment or access to mates. It is this last question that still requires answering: How are more similarly colored rivals a greater threat than more differently colored rivals? which necessitates the evolution of the behavior seen in chapter three.

Finally, my study on the causes of and potential mitigations for attrition in at-risk undergraduate students provides additional insight into the social and cognitive factors surrounding attrition from universities. The factors that differentiate between the control and the experimental groups suggest that the small class intervention provided students with the sense of community and the academic self confidence to continue in their education. I hope to continue my pedagogical research through an investigation of undergraduate research opportunities on the 1) development of scientific process skills and 2) the ability of participants to transfer scientific reasoning to a broader set of contexts.



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FEMALE *MAYLANDIA ZEBRA* PREFER VICTORIOUS MALES

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## Curriculum Vitae

### Education

Rutgers University	Ecology and Evolution	PhD	2011
Major Advisor: Dr. Rebecca Jordan			
College of William and Mary	Biology	BS	2005

### Teaching and Professional Experience

Assistant Professor (lecturer): Director of Undergraduate Advising for Biological Sciences 2011 - present  
 Mentor and Investigator: Mentorships in Life Sciences 2010 - present  
 Instructor: Portals to Academic Student Success (PASS) Rutgers, SEBS 2009 - present  
 Head Teaching Assistant: General Biology 101, Rutgers University 2008-2010  
 Assistant Head Teaching Assistant: General Biology 101, Rutgers University 2008  
 Teaching Assistant: General Biology 101 and 201, Rutgers University 2005-2008

### Publications (peer-reviewed, \* indicates undergraduate co-author)

Jordan R., **Mellor D.**, Wilt L.\*, Gershenson D\*, Howe D. (2010) Male Interaction and Mate Choice in a Group of Malaŵi Cichlids. *Ethology, Ecology & Evolution*. 22:4, 359-364.

**Mellor, D.**, Tarsiewicz, C.\*, Jordan, R. (2010): Female *Maylandia zebra* prefer victorious males. *Journal of Fish Biology*. 78: 680-687.

**Mellor D.**, Wilt L.\*, Gershenson D\*, Howe D, Jordan R. (in review): Female preference in the context of male interactions in *Maylandia zebra* of Lake Malawi.

### Publications (non peer-reviewed)

**Mellor, D.** and Jordan, R.: Why are there so many cichlids in Lake Malawi? Investigating the role of sexual selection in the Mbuna. *Buntbarsche*, American Cichlid Association.

### Research Experience and Projects

Graduate Assistant, Ecology Nature of Science, NSF Project 2009 - present  
 Researcher and Program Developer, Undergraduate Mentorship Project 2009 - present  
 Research Assistant and Programmer, Aquarium Construction Toolkit 2008 – 2010  
 Research Assistant, Sexual Selection of Lake Malawi Cichlids (Jordan Lab) 2006 - present  
 Research Assistant, Parental Behavior, Costa Rican Cichlids (Coleman Lab, CSUS) 2009-2010  
 Research Assistant, USDA Trail Conference 2008-2009  
 Field Biologist, Loon Preservation Committee of New Hampshire 2005  
 Research Assistant, NSF Research Experience for Undergraduates 2003