Aggressiveness, boldness, and lateralization: an investigation of personality by sex and alternative male morph in *Pelvicachromis pulcher*

by

Cheryl Marie Sedlak Seaver

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

Department of Psychology
University of Alberta

Abstract

Animal personality, patterns of behavior that are consistent across time and contexts, is a growing area of study and has been documented in a wide array of species. Some personality traits show sex differences. Recent work on the kribensis cichlid (*Pelvicachromis pulcher*) suggests that some variation within sex may be related to their environmental sex determination system. Little is known about personality in this species, however, in this thesis I examine the personalities of females and two alternative male morphs with respect to aggression, boldness, and lateralization. I investigate how the gender and morphs are related to personality and how the characteristics of personality intersect and interact with one another. To evaluate these characteristics I ran fish through five tests: an aggression assay, an open field exploration task, an novel environment emergence boldness task, and several cerebral lateralization tests. I demonstrate that 1) the different sexes and morphs employ different aggressive strategies; 2) there are boldness differences between the sexes, but not the morph types; and 3) there are also lateralization differences in eye use between the sexes and morphs, which are, to a certain extent, dependent upon the stimuli. These results suggest that females are very different from either male morph type particularly with regard to aggression and boldness.

Preface

This thesis is an original work by Cheryl Sedlak Seaver. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Animal Care and Use Committee, Project Name “Social Determination of Sex and Social Behaviour in a Cichlid Fish”, No. AUP0000005, June 1, 2011.

Acknowledgments

I would like to thank Peter Hurd for advising me throughout my graduate studies and for giving me the invaluable experience of learning what he had to offer including de-mystifying the seemingly magical ways of R. I also want to thank Brian Dupuis for being another source of information, as well as a great supplier of tea and the occasional nerdy social break. A great big thank you goes out to Michele Moscicki for all the support, good advice, and eagerness to make my lab experience as enjoyable as possible during my time as a graduate student. Thank you to Issac Lank and the rest of the guys in the Psych Shop (Lou Omerzu and Al Denington) for building and assembling all of the gadgets, tanks, test apparatuses, and for supplying all the silicone and batteries we could ever need for apparatus repairs and thermometers. And to Philip May for helping to salvage the data when the electronics decided they had enough.

Thank you to my committee members, Chris Sturdy and Colleen Cassady St. Clair, for your introduction to the world of Gantt charts and your sage advice. And to Jeff Bisanz: thank you for being willing and able to serve on my examination committee.

Thanks to all the Sex and Violence Lab volunteers and lab students including Owais Yahya and Narek Hakobyan who helped get this project started and for covering fish care when I couldn't. Jason Banh and Ashlesha Deshpande: thank you for your help in testing and scoring. With heartfelt gratitude I give a special thanks to Evan Zinyk, Tessa Hubbell, Kate Dawson, and Madeleine Graham for going above and beyond the call of duty and helping to figure out all the quirks of these fishes' behavior, helping to run the tests, and for taking the goop that was the data and turning it into the cleanest and finest set of numbers I've ever seen. Without all of you and your eagerness to help I could never have turned this around so speedily.

Thank you to my lovely sisters-at-arms Julia Patt, Jessica Baker, and Elizabeth Zuckerman for keeping my spirits up and making me laugh throughout the entire process despite being half a continent away. All of your wisdom, support, enthusiasm, and life experiences are energizing.

As always, thank you Greg Norman and my parents for not letting my project get the better of me and for believing in my abilities even when I had my doubts. You are my inspiration and with you all in my corner I know I can never truly fail.

Table of Contents

List of Tables

List of Figures

Aggressiveness, boldness, and lateralization an investigation of personality by sex and alternative male morph in *Pelvicachromis pulcher*

Introduction

There is extensive behavioral variation between individuals of a species and between species. Researchers have found evidence of a variety of individual differences within fish including: aggression (Ariyomo, & Watt, 2013; Earley, Hsu, & Wolf, 2000; Larson, O'Malley, & Melloni, 2006; Reddon, & Hurd, 2008; Wong & Balshine, 2011), the bold-shy axis (Brown & Braithwaite, 2004; Chapman, Morrell, & Krause, 2010; Reddon & Hurd, 2009; Scharnweber, Plath, & Tobler, 2011; and Toms et al., 2010), and behavioral lateralization (Ariyomo & Watt, 2013; Arnot, Ashton, & Elwood, 2011; Bisazza, Rogers, & Vallortigara, 1998; Cantalupo, Bisazza, & Vallortigara, 1995; Dadda, Domenichini, Piffer, Argenton, & Bisazza, 2010; Facchin, Bisazza, & Vallortigara, 1999; Reddon & Bashine, 2010; Reddon & Hurd, 2008; Reddon & Hurd, 2009; and Sovrano, Bisazza, & Vallortigara, 2001).

Aggressiveness is an animal's tendency to attack or threaten another animal independent of fighting ability or its short-term need to win (Hurd, 2006). Individuals use aggressive actions to help maintain dominance, defend territories, protect offspring, and to gain mates (Ariyomo & Watt, 2013). Aggressive actions can lead to injuries and even death (Ariyomo & Watt, 2013); with such high costs and benefits for the winners and losers, it stands to reason that actions like these ought to be under very strong evolutionary pressure. However, remarkable variation persists (Ariyomo, & Watt, 2013; Earley, Hsu, & Wolf, 2000; Just & Morris, 2003; Larson, O'Malley, & Melloni, 2006; Reddon, & Hurd, 2008; Schwartzer, Ricci, & Melloni, 2013; Wong & Balshine, 2011). Variation in aggression is an extensively explored topic in the animal literature, and shows considerable heritability and standing genetic variation (Bakker, 1985; Bakker 1986). In addition, aggressiveness is one of several personality traits that often correlates with boldness (Dingemanse et al., 2007) and with lateralization (Reddon & Hurd, 2008).

The bold-shy axis is "one of the more distinctive, heritable and stable sources of behavioral variation" (Toms et al., 2010, p. 2). It is defined variously as either the propensity to take risks (Coleman & Wilson, 1998; Toms et al., 2010) or as an individual's response to a risky situation (Reale, Reader, Sol, McDougall & Dingemanse, 2007). Since high boldness levels can influence how fast an animal approaches new objects or explores a new environment, the trade-off in fitness for being a bold or shy fish is context dependent. High predation environments are found to have fish with higher boldness scores when compared to fish from a low predation area (Brown, Jones & Braithwaite, 2005). By being bold in a dangerous environment, fish are better able to avoid starvation, even though the trade off is the potential loss of life from predation. In contrast, a shy fish in a dangerous environment might be less likely to get killed by a predator, but may be more likely to starve. Additionally, the benefits of being unique are such that a bold fish in a group of shy fish has access to the best resources, while a shy fish in a group of bold might survive longer because the bold fish are more prone to being eaten. The bold-shy axis also correlates with lateralization, but this relationship is only found when fish are exploring a familiar environment (Reddon & Hurd, 2009).

Lateralization is the “preferential use of one hemisphere of the brain for specific cognitive functions” (Reddon & Hurd, 2009, p. 189) and it appears throughout the animal kingdom. It is found in toads (Robins, Lippolis, Bisazza, Vallortigara & Rogers, 1998; Vallortigara, Rogers, Bisazza, Lippolis & Robins, 1998), birds (Diekamp, Regolin, Güntürkün, & Vallortigara, 2005), fish (Bisazza, Cantalupo, Capocchiano, & Vallortigara, 2000; Cantalupo et al., 1995; Moscicki, Reddon & Hurd, 2011; Reddon & Balshine, 2010) and humans (Bottini & Toraldo, 2003; Uttl & Pilkenton-Taylor, 2001). Among non-human animals lateralization is typically measured by eye use, while humans are more familiar with it as handedness. The benefits of lateralization is thought to be such that it allows the brain of a single organism to cope with dual tasks or conflicting bits of information in a single instance and process them simultaneously in parallel (Cantalupo et al., 1995; Vallortigara, 2000). Being able to spot a predator while approaching a potential mate would be vastly beneficial when compared to just watching the predator and losing a valuable mating opportunity or to the loss of life in pursuit of a mating opportunity. However there are potentially hazardous repercussions of lateralization such as hemineglect (Vallortigarra, 2006). Hemineglect is a type of localized blind spot where information will not result in an active response from the animal. E.g., birds that are restrained and presented with a line of food spread evenly in front of them will mainly peck on the food to their left (Diekamp et al., 2005).

In animals, lateralization can occur at an individual level or at a population level and each varies across species (Vallortigarra, 2006). Individual level biases represent an individual’s preference in lateralization, which may differ from another individual in the population either in the direction of the bias (left vs. right) or in the strength of the bias (more strongly lateralized vs. weakly). Population level biases represent the population as a whole sharing a preferential direction of a bias. A classic example of a population level bias would be the tendency of humans to be right handed and use that hand for a majority of their activities including writing. Population level biases are more commonly found in more gregarious animals (Bisazza, et al., 2000). Bisazza et al. (2000) proposed that these population level lateralization biases might provide protective benefits in large groups, such as schools of fish, as they would facilitate coordination between individuals.

In this thesis, I aim to provide an overview of how sex, color morph, and fish size are associated with differences in personalities and behavior in *Pelvicachromis pulcher*. The behaviors I focus on are aggression, boldness, and lateralization.

Materials and Methods

The species

Kribensis (*Pelvicachromis pulcher)* is a species of small freshwater cichlid fish originating from Nigeria (Nwadiaro, 1985). In most cichlid species, mature males are territorial and defend their territories either through bites or lateral displays (Heiligenberg, 1965). Kribensis establish and defend resource based territories (Linke & Staeck 1994) and are highly aggressive towards their counterparts. However, there are some unusual characteristics in addition to their location of origin and general appearance that make them distinct from their more thoroughly studied counterparts, convict cichlids (*Amatitlania nigrofasciata*). The males of this species have one of at least four distinct colorations (red, yellow, green and blue), also known as color morphs, that range along their jaws and bellies that differ between the individuals (Linke & Staeck 1994). In addition to displaying different colors on their jaws and bellies, the male morphs have different mating strategies with red males being more apt to be pair or harem keepers and yellow males being more likely to become pair or satellite males (Martin & Taborsky, 1997). However, there is very little in the literature about the blue or green morphs because yellow male morphs appear to be the more common coloration with reds being the next most frequent. Heiligenberg identified both yellow and red males in 1965, while the blue and green morphs have only thus far been photographed and described by Linke and Staeck in their book *African Cichlids I Cichlids From West Africa: A Handbook for Their Identification, Care, and Breeding* (1994).

Study population and laboratory conditions

I used 174 kribensis in this experiment: 61 females and 113 males. None of the fish had any previous experience with any of the tests described below. Juvenile and adult kribensis were obtained from local suppliers and housed in a mixed sex stock tank until they were judged to be adults. Water temperature was maintained at 25±2 °C and overhead lighting provided a 12:12hr light:dark cycle for all tanks. Fish were fed once a day *ad libitum* for five days a week with either frozen brine shrimp or dried flake food. Adult fish were identified by colorful displays and by their establishment and guarding of territory. Fish to be tested were housed with one fish per section in six smaller sections each 16 cm × 12 cm × 27 cm of 30-L tanks (50 cm × 27 cm × 30 cm) with alternating males and females such that each fish saw at least one fish of the opposite sex and of the same sex in the adjacent sections. Fish acclimated to their new housing for a least one-week prior to testing and they were also provided a minimum of a one-week break between tests.

Size measures

Adult male kribensis are generally longer than females, reaching as much as 10 cm in the wild while females can grow up to 7 cm (Linke & Staeck, 1994). Therefore, I expected that the males in my study would, in general, be a larger size than the females. Fish were measured for standard length (distance from fish mouth to the base of the tail) and mass after each test. Fish condition (the distance from the coordinates of the fish's mass and standard length to the point on the regression line based on mass) was calculated from the measurements taken.

Measures of aggression

Fish were tested for aggression using a modified version of Reddon and Hurd's (2008) design, using mirror image simulation in a 30-L tank (50 cm × 27 cm × 30 cm) with mirrors at both ends behind black opaque doors. The tank was divided into two equal-sized compartments (25 cm × 27 cm) by a white opaque wall and each had a piece of PVC piping or a plant for shelter and filled to a depth of 11 cm. Trials consisted of a single fish acclimatizing in one of the two compartments for 24 hours, followed by the remote raising of the black opaque barrier. The fish were videotaped using a Rollei HD3" LCD Touch (Movieline P5, Hamburg, Germany), Sony HandyCam (DCR-SX22, Sony, Tokyo, Japan), or JVC Hard Disk Camcorder (G2-MG330HU, JVC Canada Inc., Ontario, Canada) from the side interacting with their mirror image for an hour.

The videos were scored using JWatcher (Blumstein et al. 2010). Fish were scored on four behaviors deemed to be aggressive: biting the mirror, charging the mirror (identified by a quick darting motion towards the mirror), fanning out their dorsal and ventral fins in a lateral display, and beating the mirror with their tails (tail beating). The start time of each aggressive action was coded, the type of aggressive action, and the duration of that aggressive action. From this coding it was also possible to measure the latency from when the mirror was exposed to the fish's first aggressive action. Fish that did not engage in aggressive behavior were given maximum latency times of 3600s.

Measures of boldness

Fish were tested for boldness in an open field task following a modified version of Champagne, Hoefnagels, de Kloet, and Richardson's (2010) design. The task consisted of a 38-L (50 cm × 27 cm × 30 cm) tank filled to a depth of 22 cm with a plastic sheet with grid marks laid out under the tank dividing the tank into 50 equal sized squares (5 cm × 5 cm). Fish were acclimatized in a circular piece of PVC piping (10 cm × 8 cm) with a lid centered in the middle of the tank for two minutes and then the PVC piping starting box was lifted out remotely and the fish were video taped using a webcam (Logitech Quickcam V-UVB49, Logitech, Apples, Switzerland) and Cheese (2.30.1, Siegel, 2007) or Logitech ® webcam software (12.10.1113.0000, Logitech, Apples, Switzerland) swimming about the tank for five minutes.

The videos were scored using JWatcher (Blumstein et al. 2010). Fish were scored on the total time spent in each of the middle, edge, and corner squares and the number of squares entered for each of middle, edge, and corner squares. The proportion of each type of square was calculated by dividing the number of squares entered for a given type by the total number of squares entered over the duration of the trial. An additional measure dubbed "the freak-out period" was recorded, and this was calculated by taking the amount of time from when the fish was released to when a fish first spent one entire second in any square. The final measure calculated was the number of squares entered during "the freak-out period" and this consisted of the number of squares that the fish crossed into during their "freak-out period." For the open field analysis, one fish (a yellow morph) was excluded due to technical difficulties while running. This reduced the overall number of fish analyzed to 136 (69 yellow males).

Fish were also tested in the novel environment task a week after their test in the open field. The novel environment task followed a modified version of Brown, Burgess, and Braithwaite's (2007) and Reddon and Hurd's (2009) methodology consisting of a 38-L (50 cm × 27 cm × 30 cm) tank filled to a depth of 11 cm. An opaque Plexiglas box (12 cm × 13 cm × 12 cm) with no ceiling and a removable door at one end was placed in the center of one end of the tank (about 5 cm out from the end of the tank). Subjects were allowed to acclimate for two minutes in the Plexiglas box prior to testing; each subject received between one and 10 videotaped trials (using the JVC or Rollei camcorders) with a cut off time of 20 minutes for each trial. If the fish did not to emerge within the 20 minutes, then the fish was given two days off before being tested again.

Boldness was measured by timing how long it took the fish to emerge from the Plexiglas box shelter into the novel environment (Brown et al., 2007). For the cases where the fish took more than one trial to emerge the total time for each trial was summed together to get a measure of boldness. If the fish failed to emerge on all 10 trials, the fish was given a capped emergent time of 12,000 seconds.

Measures of lateralization

The octagonal mirror task used a modified apparatus and procedure of Moscicki, Reddon, and Hurd's (2011) design. The apparatus consisted of a large square aquarium (74 cm × 74 cm × 38 cm) containing eight square mirrors (30 cm × 30 cm) arranged in an octagon. A circular piece of opaque PVC piping, with a diameter of 8 cm, was centered in between the centered internal octagon (41 cm × 41 cm × 20 cm) made of eight opaque Plexiglas rectangles (17cm × 20 cm) and the external mirror octagon. The apparatus was filled with water to a depth of 11 cm. Trials consisted of a two minute acclimation period followed by the remote lifting out of the PVC piping start box and a 10 minute session photographed from above, every two seconds, using a webcam (Logitech Webcam V-U0003, Logitech, Apples, Switzerland) and Cheese (3.6.2, Siegel, 2007).

Pictures were scored on the number of pictures the fish had a particular eye facing the mirror, the number of pictures where the fish did not move, the number of pictures where the fish could be looking at the mirror with both eyes and the number of pictures where the fish was facing away from the mirror or not visible to the webcam. Lateralization indices were calculated by subtracting the total number of left eye viewings from right eye viewings and divided by the total number of either eye use (not including the cases where both eyes could have been used). Absolute lateralization indices were calculated by taking the absolute value of the lateralization indices.

The circular lateralization task is a heavily modified version of the mirror octagon task designed in our lab. A square white Plexiglas tank (74 cm × 74cm × 39cm) containing three concentric circular rings (diameters 71cm, 42 cm, and 20 cm) with only the external ring made of opaque Plexiglas, the two internal concentric rings are comprised of clear Plexiglas. A circular piece of opaque PVC piping, with a diameter of 8 cm, was centered in between the 42 cm clear and 71 cm opaque Plexiglas circular rings. Trials consisted of inserting three stimuli test fish of the same sex into the center ring, allowing the fish to acclimate for three minutes prior to depositing the test fish into the start box and allowing this fish to acclimate for two minutes. Following acclimation, the door to the tank was remotely opened and fish were photographed from above, using a webcam (HD Webcam V-U0023) and Cheese (3.6.2, Siegel, 2007), for 10 minutes with a picture taken every two seconds. Each fish was tested in the apparatus twice – once with male stimuli fish and once with female stimuli fish with at least a one-week break between tests. The stimulus fish were each given a two-day break between testing.

Individuals were scored on the number of pictures the fish had a particular eye facing the stimulus fish in the center, the number of pictures where the fish did not move, number of pictures where the fish could be looking at the stimulus fish with both eyes and the number of pictures where the fish was facing away from the stimulus fish or not visible to the video camera. Lateralization indices (LI) were calculated by subtracting the total number of left eye viewings from right eye viewings and divided by the total number of either eye use (not including the cases where both eyes could have been used or not visible to the camera). Absolute lateralization indices (ALI) were calculated by taking the absolute value of the LI.

Morph identification

After the fish had been run through all the tests, they were sacrificed. Their heads were placed in a 4% paraformaldehyde solution for male color morph identification. Fifteen red males were identified in the sample along with seventy yellow males, confirming my expectation that the yellow males would be the more predominant morph color. An additional, and surprising, two blue morphs were identified in this same manner; they are included in the graphs, but are excluded from the analyses. Thirty-six fish died during testing and one was removed from testing due to experimenter error early in testing, eleven females and twenty-six males in total, these fish are excluded from all analyses.

Data Analysis

All analyses were performed using R v. 2.13.1 (R Development Core Team, Vienna, Austria). Analyses of covariance (ANCOVA) were performed using the aov() function from the stats library (version 2.13.1) to identify any effects of size on the behavioral outcomes. Analyses of variance (ANOVA) were used to determine if there were differences between females, yellow males, and red males. Post-hoc comparisons were conducted using the pairwise.t.test() function from the stats library (version 2.13.1) with pooled standard deviation. A Pearson's chi-squared test was performed using the chisq.test() function from the stats library (version 2.13.1) to identify if there were differences in aggression among females, yellow males, and red males. Additionally a permutational multivariate analysis of variance was run using the adonis() function from the vegan library (version 2.0-2) on the outcome measures to identify what independent variables best explained the data.

Results

Size measures

I found that standard length and mass were highly related to fish sex and color morph throughout testing and were not producing a biasing effect on the behaviors tested. Fish ranged from 1.02 to 4.26 grams in mass (Mean ± SD: Females = 1.82g ± 0.29g; Yellow males = 2.44g ± 0.53g; Red males = 2.11g ± 0.29g) and 3 to 6.4 cm in length (Mean ± SD: Females = 3.8cm ± 0.2cm; Yellow males = 4.4cm ± 0.3cm; Red males = 4.2cm ± 0.3cm).

Aggression

The results of whether the fish were aggressive or not (as measured by whether they made an aggressive move towards the mirror or not) shows that a higher percentage of males perform aggressive actions when compared to females (Females: 58% aggressive; Yellow males: 72.9% aggressive; Red males: 73.3% aggressive, $X^2(2, 133) = 3.86$, $p = 0.15$). Latency to first aggressive act ranged from 1s to the end of test time (3600s) and differed significantly between the groups (*F*(2, 132) = 3.19, *p* = 0.04, Figure 1). Yellow males were significantly faster to their first aggressive action than females (*p* = 0.01, Figure 1).

The number of bites ranged from 0-1529 (Mean ± SD: Females = 232.76 ± 295.5; Yellow males = 309.31 ± 311.40; Red males = 438.47 ± 496.45) and the time spent performing bites ranged from 0-1305.2s (Mean ± SD: Females = 198.79s ± 231.36s; Yellow males = 293.81s ± 303.54s; Red males = 360.97s ± 401.03s; F(2, 132) = 2.44, *p* = 0.09, Figure 2). The number of bites was not significantly different between the groups (*F*(2, 132) = 1.85, *p* = 0.16, Figure 2).

The number of charges ranged from 0-40 (Mean ± SD: Females = 3.88 ± 6.80; Yellow males = 6.74 ± 8.42; Red males = 9.93 ± 12.82). The number of charges did reveal differences between the groups (*F*(2, 132) = 3.45, *p* = 0.03, Figure 2). Red males performed significantly more charges than did the females (*p* = 0.02, Figure 2), while yellow males trended towards charging significantly more than females (*p* = 0.07, Figure 2).

The number of lateral displays ranged from 0-42 (Mean ± SD: Females = 3.08 ± 5.59; Yellow males = 3.51 ± 6.87; Red males = 1.80 ± 1.78). The number of lateral displays was not significantly different among the groups (*F*(2, 132) = 0.50, *p* = 0.61, Figure 2).

The number of tail beats ranged from 0-51 (Mean ± SD: Females = 1.80 ± 7.57; Yellow males = 4.64 ± 8.22; Red males = 9.87 ± 13.10; *F*(2, 132) = 5.23, *p* = 0.006, Figure 2). Red males performed significantly more tail beats than either yellow males or females (yellow morph: *p* = 0.04 and females: *p* = 0.002, Figure 2) and yellow males trended towards performing significantly more tail beats than females (*p* = 0.08). Overall, females were less aggressive and slower to an initial aggressive response than males and there are observed preferences for different aggressive actions based on the gender or color morph of the fish.

Boldness

There was a non-significant trend towards different activity levels in the three groups (*F*(2, 131) = 2.89, *p* = 0.06, Figure 3). The amount of time spent in corner squares ranged from 0-304.8s (Mean ± SD: Females = 161.38s ±102.79s; Yellow males = 142.04s ± 83.44s; Red males = 147.86 ± 103.57), while time spent in edge squares ranged from 0-321.7s (Mean ± SD: Females = 128.70s ± 107.96s; Yellow males = 128.13s ± 73.97s; Red males = 150.01s ± 103.96s), and time spent in middle squares ranged from 0-300s (Mean ± SD: Females = 8.36s ± 18.17s; Yellow males = 26.36s ± 62.53s; Red males = 2.08s ± 4.16s). The groups did not differ in the amount of time spent in either corner or edge, or middle squares (corner: *F*(2, 131) = 0.63, *p* = 0.54 and edge: *F*(2, 131) = 0.37, *p* = 0.69 respectively, Figure 4). However, females spent less time in middle squares than yellow males (*p* = 0.04, Figure 4).

For the novel environment analysis, three female fish and one yellow morph were excluded from the novel environment emergence task due to technical difficulties and experimenter error during testing reducing the overall number of fish analyzed to 133 (47 females and 69 yellow males). The amount of time it took for fish to leave the start box ranged from 0.1 to the maximum time of 12000s (Mean ± SD: Females = 3255.63s ± 4135.08s; Yellow males = 748.01s ± 947.60s; Red males = 778.61s ± 790.72s) and was significant (*F*(2, 128) = 14.02, $p < 0.001$, Figure 5). Females emerged significantly more slowly than males (yellow males: *p* = 0.002 and red males: $p < 0.001$) and the male morphs did not differ from each other (*p* = 0.97, Figure 5).

In general the results show that the fish preferred to spend their time in the corner and edge squares as compared to the middle squares (Mean ± SD: Corner time = 149.91s ± 93.08s; Edge time = 130.79s ± 90.97s; Middle time = 16.93s ± 47.13s) and the total number of squares entered during the open field exploration task ranged from 1-270 (Mean ± SD: Females = 50.30 ± 49.11; Yellow males = 75.38 ± 61.66; Red males = 80.00 ± 86.76).

Lateralization

None of the three groups showed a population level lateralization in the mirror octagon task (*t*-test: Female: *t*(49) = -1.03, *p* = 0.31; Yellow males: *t*(69) = -0.05, *p* = 0.96; Red males: *t*(14) = 1.50, *p* = 0.16) nor was there a significant difference tween groups in the LI (*F*(2, 132) = 0.55, *p* = 0.58). Conversely, the ANOVA on ALI with respect to color did reveal differences in the strength of lateralization between the groups (*F*(2, 132) = 5.88, *p* = 0.004, Figure 6). Pairwise *t*-tests revealed that females were more strongly lateralized than red males (*p* = 0.002, Figure 6) and yellow males were also more strongly lateralized than red males (*p* = 0.002, Figure 6) but females and yellow males did not differ (*p* = 0.87, Figure 6).

Due to the method of testing circular lateralization, my analyses examined two sets of comparisons and both comparisons were made for LI and ALI outcome measures separately. The first comparisons were based on the sex of the stimulus fish encountered in the task. The second comparisons were based on whether the stimuli fish were the same or different sexes from the experimental fish for each LI and ALI outcome measures.

It was necessary to exclude two females from both of the circular lateralization tasks and one red morph from the female circular lateralization task as a result of experimenter error. This reduced the total number of fish in the male stimulus and same-sex stimuli test conditions to 135 fish (48 females) and reduced the total for the female stimulus and opposite sex test conditions to 134 fish (48 females and 14 red males). It should also be noted that due to the limited supply of male fish the male stimuli presented to the experimental fish could be any morph type.

There were no differences among the groups with respect to the LI with male stimulus fish ($F(2, 130) = 0.30$, $p = 0.74$) or female stimulus fish ($F(2, 129) = 0.51$, $p = 0.60$). Single-sample t-tests on each group revealed that none of the group LIs differed from 0 for the test with male stimulus fish (t-test: Female: $t(47) = -0.79$, $p = 0.43$; Yellow males: $t(69) = -0.29$, $p = 0.77$; Red males: $t(14) = 0.93$, $p = 0.37$) nor with the female stimulus fish (t-test: Female: $t(47) = -0.06$, $p = 0.95$; Yellow males: $t(69) = -1.45$, $p = 0.15$; Red males: $t(13) = -1.54$, $p = 0.15$).

The groups differed significantly for ALI with male stimulus fish ($F(2, 130) = 4.14$, $p = 0.02$, Figure 6). Females and yellow males were both more strongly lateralized than red males (pairwise t-test: $p = 0.03$ and $p = 0.005$ respectively, Figure 6). The groups also differed significantly for ALI with female stimulus fish ($F(2, 129) = 3.29$, $p = 0.04$, Figure 6) where again yellow males were more strongly lateralized than red males ($p = 0.02$, Figure 6). However, in this case females and red males did not significantly differ from each other ($p = 0.14$, Figure 6).

When eyeing fish of the same sex neither the females or either male morphs differed significantly from each other in which eye they preferred to view the stimulus fish ($F(2, 130)= 0.16$, $p = 0.85$, Figure 6) nor did they reveal any differences when eyeing fish of the opposite sex ($F(2, 129)= 0.04$, $p = 0.96$, Figure 6). Again the group LIs when faced with fish of the same sex did not differ from 0 (t-test: Female: $t(47) = -0.06$, $p = 0.95$; Yellow males: $t(69) = -0.29$, $p = 0.77$; Red males: $t(14) = 0.93$, $p = 0.37$) nor when faced with fish of a different sex did the LIs differ from 0 (t-test: Female: $t(47) = -0.79$, $p = 0.43$; Yellow males: $t(69) = -1.45$, $p = 0.15$; Red males: $t(13) = -1.54$, $p = 0.15$).

When faced with stimulus fish of the same sex the ALI differed significantly among the groups ($F(2, 130) = 6.17$, $p = 0.003$, Figure 6). Yellow males were more strongly lateralized than either females (pairwise t-test: $p = 0.01$) or red males ($p = 0.003$, Figure 6), whereas females and red males were no different from each other ($p = 0.20$, Figure 6). When eyeing stimulus fish of the opposite sex, the ALI trended towards significance (*F*(2, 129) = 3.03, *p* = 0.052, Figure 6). An examination of the pairwise comparisons revealed that red males were more weakly lateralized than either females (*p* = 0.02, Figure 6) or yellow males (*p* = 0.02, Figure 6) with yellow males and females not differing from each other (*p* = 0.82, Figure 6).

Permutational Multivariate Analysis of Variance

I ran several PERMANOVAs in R (using the R package vegan, function adonis) using different variable of step-wise entry. I tested the standard length, mass, and fish condition (all measured at the time of testing in the mirror aggression task) along with the sex and color morph with respect to all of my behavioral outcome measures. The sex and color morph variable was significant regardless of the order of entry (Table 1, Table 2, Table 3), while fish condition was non-significant regardless of the order (those tables are not included). Standard length showed a significant effect if it was entered before the sex and color morph variable (Table 2). This became a non-significant trend when mass was the first variable loaded into the PERMANOVA. Mass effects were only significant when entered into the model before both the standard length and sex and color morph variables (Table 3).

The PERMANOVA results indicated that standard length and fish sex and color morph are the main independent variables most closely associated with the behavioral outcomes. Since standard length and fish sex and color morph co-vary, it is not surprising that an order effect appears since fish sex and color morph can explain all of the same variance that standard length or mass and explain more.

Discussion

Size Measures

The sex and color groups differed in both size and behavior. Standard length and mass were found to be significantly different between the sex and color morphs across all tests, however, not all the pairwise *t*-tests revealed differences. At the beginning of testing in the mirror aggression and open field boldness tasks, females and red males were fairly similar in mass to one another. However, females weighed significantly less and were shorter than either male morph by the end of testing. Alternatively, the red males were shorter and weighed less than the yellow males at the beginning of testing, which was unexpected, and were about the same mass and length by the end of testing.

Aggression

Kribensis used bites as the most prevalent form of aggressive action (Figure 2a). Contrary to what Reddon and Hurd (2013) found, females bit less than males (Figure 2a). Females were also slower to perform a first aggressive action than yellow males (Figure 1) and generally performed fewer of the other aggressive actions when compared to males (Figure 2b, c, & d). Females were also more evenly split between aggressive and non-aggressive (58% were aggressive) when compared to yellow males (72.9% aggressive) or red males (73.3% aggressive). Taken together, these results suggest that females were actually less aggressive than males.

Red males performed more tail beats than either females or yellow males (Figure 2d). They also performed fewer displays. Based on just the counts of tail beats the red males appeared to be slightly more aggressive than the yellow males, but the results of the other behavioral outcomes of the aggression task suggest that there were very few differences with respect to aggression between yellow and red males. The two blue morphs, which we included on the bar graphs (as gray dots) but not in the analyses due to small sample size, did not perform any aggressive actions during their trials.

The results suggest that there may be different aggressive strategies for the sexes and color morphs. Generally speaking, the fish seemed to prefer (in order of preference) biting then charging. Whether a fish preferred to use lateral displays or tail beats next depended on their sex or color morph. Females were least likely to use tail beats, and only slightly more inclined to use lateral displays and charges. Yellow males seemed fairly even in their use of the other three aggressive actions. Red males used the more escalated charging and tail beats and rarely used lateral displays (Jakobsson, Radesäter, & Järvi, 1979; and Enquist & Jakobsson, 1986).

These observed preferences for one type of behavior over another may be due to biological differences. The red morph could already have a lateral display advantage in the form of his red coloring. This may act as a natural deterrent to a territory invader, whereas females and yellow males do not have that distinct advantage and need to show off their size/capabilities through other means. If the red morph feels less inclined to use lateral displays to deter intruders, he may devote more of his energy to performing aggressive actions to drive off the intruder. Females and yellow males may be forced to split more of their time and energy between their aggressive actions, as they feel the need to include displaying.

Alternatively these behavior differences could be due to the fact that they differ in aggressiveness and the escalation of aggressive activities. The red morphs could be using the actions that escalate a fight more rapidly than females

Boldness

In the open field test of boldness, males entered more squares on average than females (Figure 3). The proportion of squares entered was fairly consistent across the groups. Time spent in these squares also showed that fish spent most of their time in corner and edge squares, while they spent very little of their time in middle squares. Yellow males seemed to spend more time in the middle squares compared to females or red males (Figure 4). These results provide some (although not strong) support for my hypotheses that fish prefer to spend time in the corner and edge squares and that males exhibit more exploratory behavior (Figure 3).

The novel environment emergence task revealed that females were much slower to emerge into the novel environment than males (Figure 5), which was expected. Some females took as many as 10 repetitions of testing and still did not emerge, so they received a capped value of 12,000s, which potentially drove their average time up. The male color morphs did not differ in their times to emerge.

Lateralization

The octagonal mirror task operated as a perceived social setting to test lateralization. As expected, the results showed no population level preferences for left or right eye viewing. Likewise, under the circle lateralization task, no matter what the stimulus (male, female, same-sex, or opposite sex), the experimental fish showed no population level preferences for viewing the stimuli.

When looking at the absolute lateralization measures (the strength of the lateralization and a measure of the individual level lateralization) for each of these tasks and conditions, population differences emerged (Figure 6). In the mirror octagon task females and yellow males were demonstrably more strongly lateralized than the red males (Figure 6a). In the circular lateralization task, we saw similar results when the stimuli were males or of the opposite sex (Figure 6b & d). Interestingly, yellow males were more strongly lateralized than either females or red males when viewing stimuli fish of the same sex (Figure 6e) and more strongly lateralized than red males when viewing female stimuli (Figure 6c).

These findings suggest that females and yellow males were similar in that they were strongly lateralized when viewing their mirror image in a perceived social environment (same-sex), when viewing stimuli males, or when viewing stimuli fish of the opposite sex. Interestingly, even though the mirror image provides a same-sex-viewing situation, the difference between viewing a mirror image and live fish did result in a difference in the strength of lateralization since yellow males were more strongly lateralized than even females when viewing live fish of the same sex. This suggests that the difference between live and a mirror-induced social environment was rather large. I speculate that the difference was primarily due to the behaviors of the live fish, which probably act differently than a fish's mirror image.

This still begs the question: what benefits do the fish get for being more strongly lateralized in such a manner? It is possible that yellow males need to be more strongly lateralized to better process competing information in order to be more competitive with red males for breeding opportunities. Red males may instead have the distinct benefit, by not being strongly lateralized, of being able to process information equally from both eyes. This would enable them to scan for potential breeding partners or threats regardless of the field of view. Females and yellow males could be similarly lateralized when regarding fish of the opposite sex so that when they approach each other head on they have the other in the field of view that is best for processing potential mating partners. The same reasoning could be used as to why yellow males are strongly lateralized when regarding males as well (which would again be the opposite sex for females), although it would suggest strong lateralization with regards to another threat.

In convict cichlids, parental roles are shared with males preferring to do more of the defense rather than brood care and females preferring to do more of the brood care than defense (Snekser & Itzkowitz, 2014). This appears to be very similar to how kribensis share their roles. Perhaps this division of labor sheds more insight into the lateralization preferences. Females may be lateralized in this manner so that they can continue to keep a close eye on their offspring (perhaps the opposite eye) while guarding against a threat from a male using the other eye. This could suggest that female lateralization comes about as a response to male lateralization, since a majority of the males are strongly lateralized. However, were that to be the case I would expect to see more population level biases in the directional lateralization (left vs. right) rather than individual level biases (strength). Red males would then be preferred for nest defense, as they would have the advantage by not being strongly lateralized and thus able to detect and deter potential threats from conspecifics to their offspring from all angles–regardless of the conspecific’s sex.

Permutational Multivariate Analysis of Variance

The permutational analysis of variance (PERMANOVA) offers an alternative means of examining what independent variables are most related to the behavioral outcomes measured in this thesis. By running several PERMANOVAs with different variable of step-wise entry, I was able to determine that fish sex and color morph are not only the variables that explain the variability of the behavioral outcome measures, but are also unsurprisingly related to measures of fish size. Fish condition, unsurprisingly, is not a good predictor of the behavioral outcomes, nor are the interactions of fish standard length, mass, or sex and color morph.

This raises the question of which comes first in the life of a fish. Does sex determination occur before fish size varies or does fish size vary first and play a role in sex determination regardless of environmental factors? Add in the potential for environmental sex determination in this species and the question of order is further confounded.

Conclusion

Looking at the results across the measures of aggression, boldness, and lateralization a few trends emerged. Females differ from both male morph types with respect to aggression, activity, and boldness; they are both less aggressive, less active, and less bold than males. Among the male morphs, there are few differences in these measures. Red males appear to be slightly more aggressive than yellow males, as evidenced by their use of tail beats and charges in the mirror aggression task. Yellow males seem bolder than the red males as they spend more time in the middle squares in the open field task. At the individual level, the yellow males and female both show indications of individual lateralization, whereas the red males do not.

The pattern of aggression and boldness in females and males could be something that comes about from the preferential division of labor amongst kribensis. Males that patrol their territory could be more bold and be more aggression to defend their territory, mate, and offspring. Alternatively, females being less bold and aggressive would be more suited to more closely guarding the nest site, which is generally hidden, and so would potentially see a lower need for aggression and administering more of the brood care behaviors (Snesker & Itzkowitz, 2014). Additionally, the preferential parental role of kribensis could also shed some light on the pattern of ALI scores for the genders and male morphs. Female absolute lateralization may be more suitable for keeping one eye on their offspring while using the other eye to look for threats. Red males may have an advantage when it comes to nest defense over yellow males by not being strongly lateralized one way or another and so may be better suited to territory patrolling and defense further away from the nest site. The current patterns would suggest that yellow males would then be more like females and would perform their guarding duties close to the nest since they are also strongly lateralized. The caveats of this explanation are twofold. I would expect yellow males to exhibit more charging aggressive behaviors to make up for their lack of patrolling. I would also, possibly, see less displaying behaviors since displaying could be more of a patrolling behavior to discourage others from invading the territory. However, this does not seem to be the case.

The PERMANOVA validated that fish sex and color morph, standard length, and mass were strongly related to the behavioral outcome measures explored in my study. It also revealed that most of the variability explained by standard length and mass can be accounted for by the sex and color morph. As previously noted, we cannot say definitively which qualities (sex, size, etc.) develop first in fish and most influence behavior.

Future research could expand upon this wealth of knowledge by including a larger sample size of red males and including more green and blue morph males to make further comparisons between the male color morphs. Additionally, testing the males to determine what mating strategies they employ would possibly help explain the differences between color morphs and possibly identify why yellow males differ from females. Martin and Taborsky (1997) identified red males as equally likely to be either harem or pair males, while yellow males were unequally split between being pair and satellite males, with the majority being satellite males. These breeding strategies, however, do not appear to be fixed for life as Martin and Taborsky (1997) noted that fish did change mating strategies in their study.

Further research could also better identify what determines the alternative morphs in males and why the blue and green morphs are so rare. Martin and Taborsky (1997) and Heiligenberg (1965) proposed that the color morphs are genetically determined, but there is some evidence they are actually determined by the same mechanisms that are involved in environmental sex determination (Reddon & Hurd, 2013). Heiligenberg (1965) identified that kribensis are subject to environmental sex determination and Rubin (1985) found further evidence that low pH values skews the sex ratio to be predominantly male. However, Reddon and Hurd (2013) found that the male biasing pH value of 5.5 also produced more red males than yellow males. While this type of research has provided researchers with foundational evidence for environmentally determined color morph, the same cannot be said of the blue and green morphs. Perhaps a specific combination of environmental conditions (temperature has also been recognized as another environmental sex determining factor in many species of chiclids; Ospina-Álvarez & Piferrer, 2008; Römer & Beisenherz, 1996) produces blue or green morphs. Or there might be some additional genetic component to the color morphs which could explain the blue and green morphs rarity.

With the new found understanding of kribensis behavior, researchers can now look to investigating environmental sex determining mechanisms and sexual dimorphism within these fish and question how environmental sex determination might also affect individual personality (Espinoza, 2011). Kribensis can be viewed as a gender continuum with very aggressive and bold males representing the almost “hyper” male type (possibly red males) on one end and extremely shy and non-aggressive females on the other (the hyper females type) and varying degrees of female or male behavior in between. With such a visual and physical representation of the gender continuum this would enable us to investigate a non-human model for why different degrees of feminine or masculine behavior occur in human populations regardless of the base sex. Furthermore, with the potential for these sexes and color morphs to exhibit different coping strategies, we may also find we have an animal model that would enable researchers to see if these different coping strategies are sexually dimorphic as well.

Table 1. PERMANOVA with fish sex and color morph as the initially loaded variable.

	df	***F***	***p***
(A) Sex and color morph	2	12.58	0.010
(B) Mass	1	0.54	0.55
(C) Standard length	1	0.68	0.42
B x C interaction	1	0.13	0.78
A x C interaction	2	-0.06	0.98
A x B interaction	2	1.61	0.21

Table 2. PERMANOVA with fish standard length as the initially loaded variable.

	df	***F***	***p***
(A) Standard length	1	8.56	0.010
(B) Mass	1	0.19	0.81
(C) Sex and color morph	2	8.83	0.010
A x B interaction	1	0.13	0.85
A x C interaction	2	-0.06	0.98
B x C interaction	2	1.61	0.14

Table 3. PERMANOVA with fish mass as the initially loaded variable.

	df	***F***	***p***
(A) Mass	1	4.25	0.020
(B) Standard length	1	4.49	0.08
(C) Sex and color morph	2	8.83	0.010
A x B interaction	1	0.13	0.80
B x C interaction	2	-0.06	0.98
A x C interaction	2	1.61	0.22

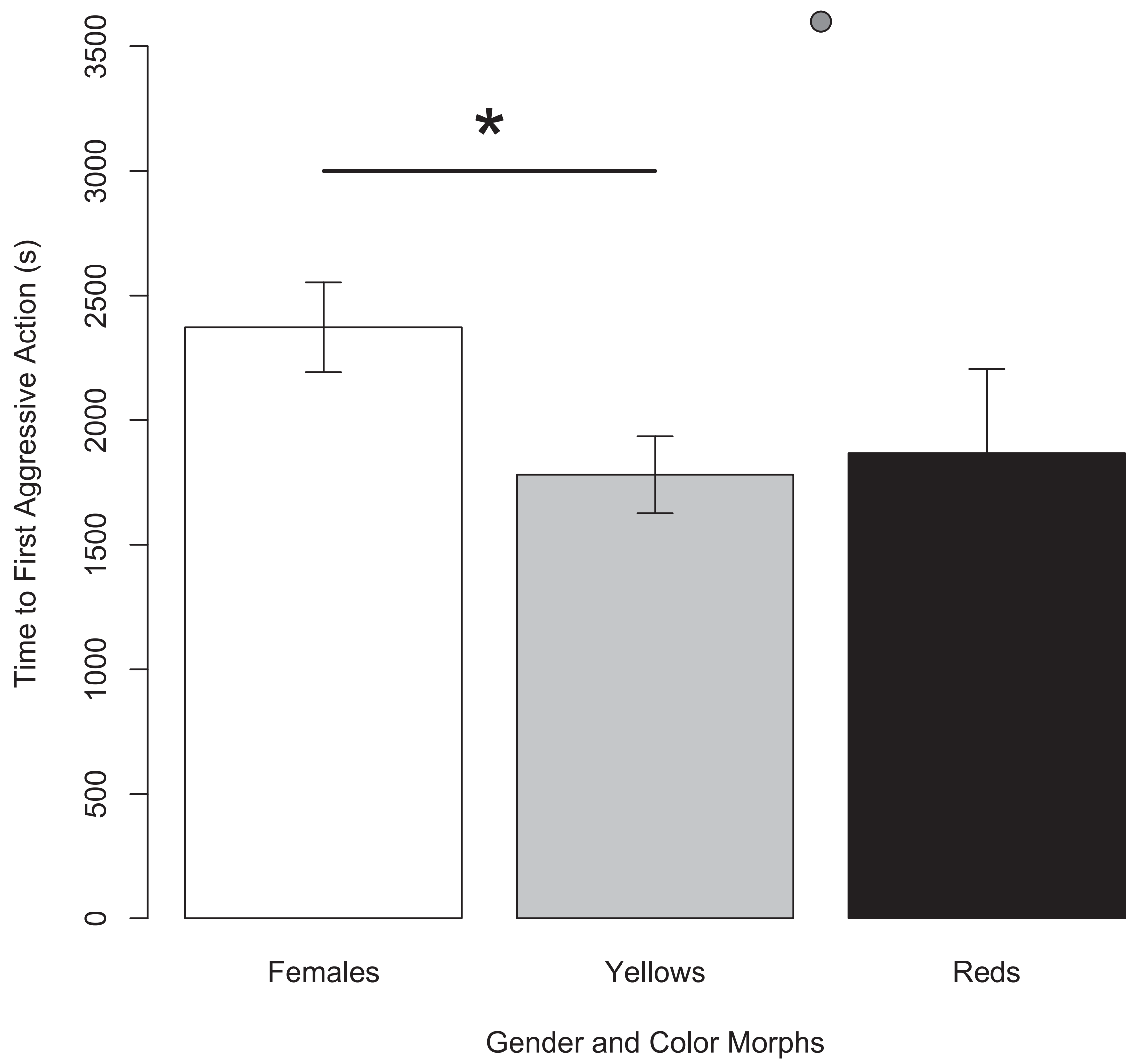

Figure 1. Female and male color morph times to first aggressive action in the mirror aggression task. Mean (± SEM) times to first aggressive action for females (white bar), yellow male morphs (gray bar), and red males (black bar). Females are significantly slower to perform an aggressive action against a mirror opponent as compared with yellow male morphs ($p = 0.01$).

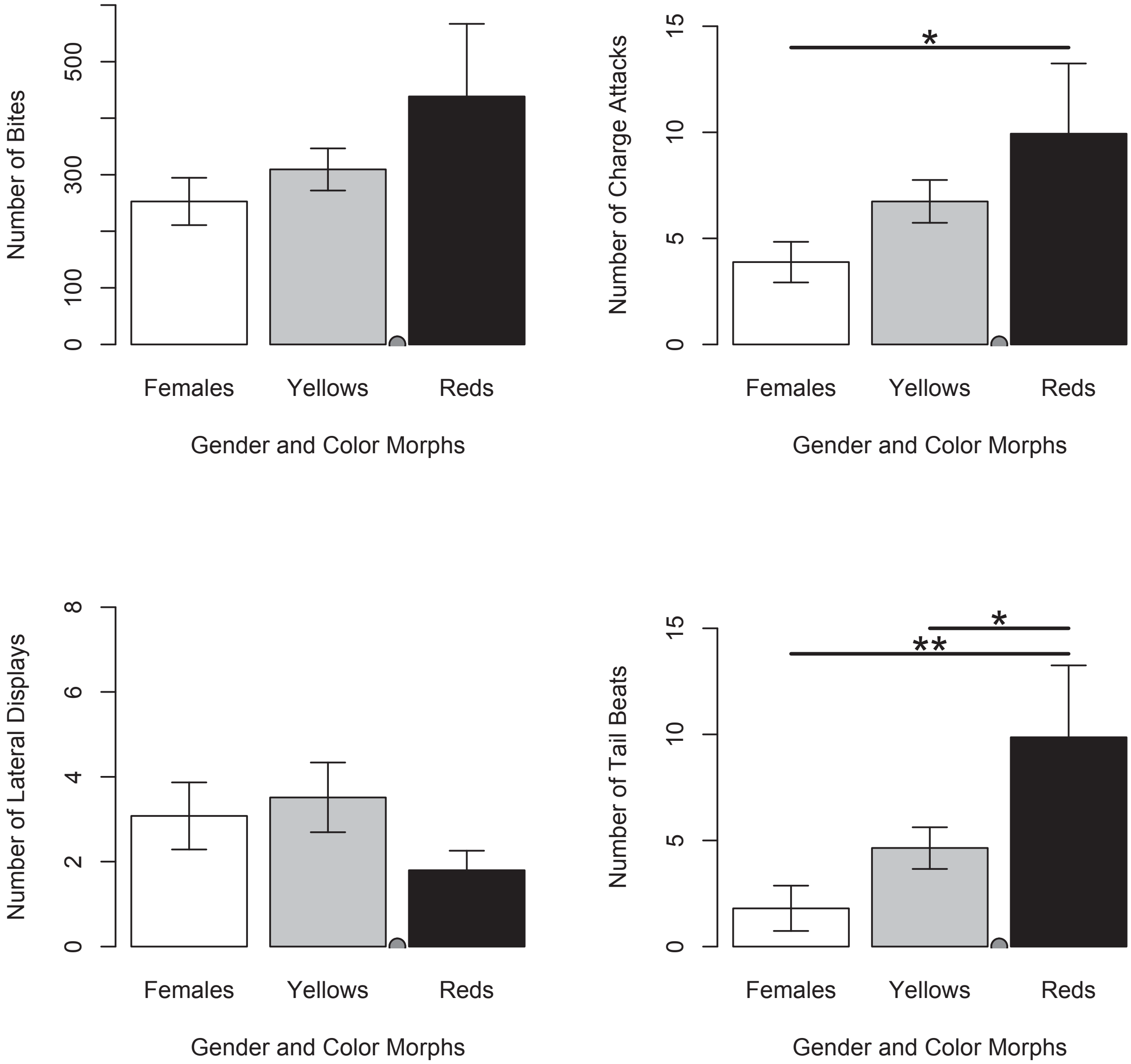

Figure 2. Female and male color morph counts of specific aggressive behaviors during the mirror aggression task. Mean (±SEM) counts of bites (a), charges (b), lateral displays (c), and tail beats (d) at their mirror image. Females perform significantly less charge ($p = 0.02$) and tail beat ($p = 0.002$) attacks as compared to red males. Yellow males also perform significantly fewer tail beats than red males ($p = 0.04$).

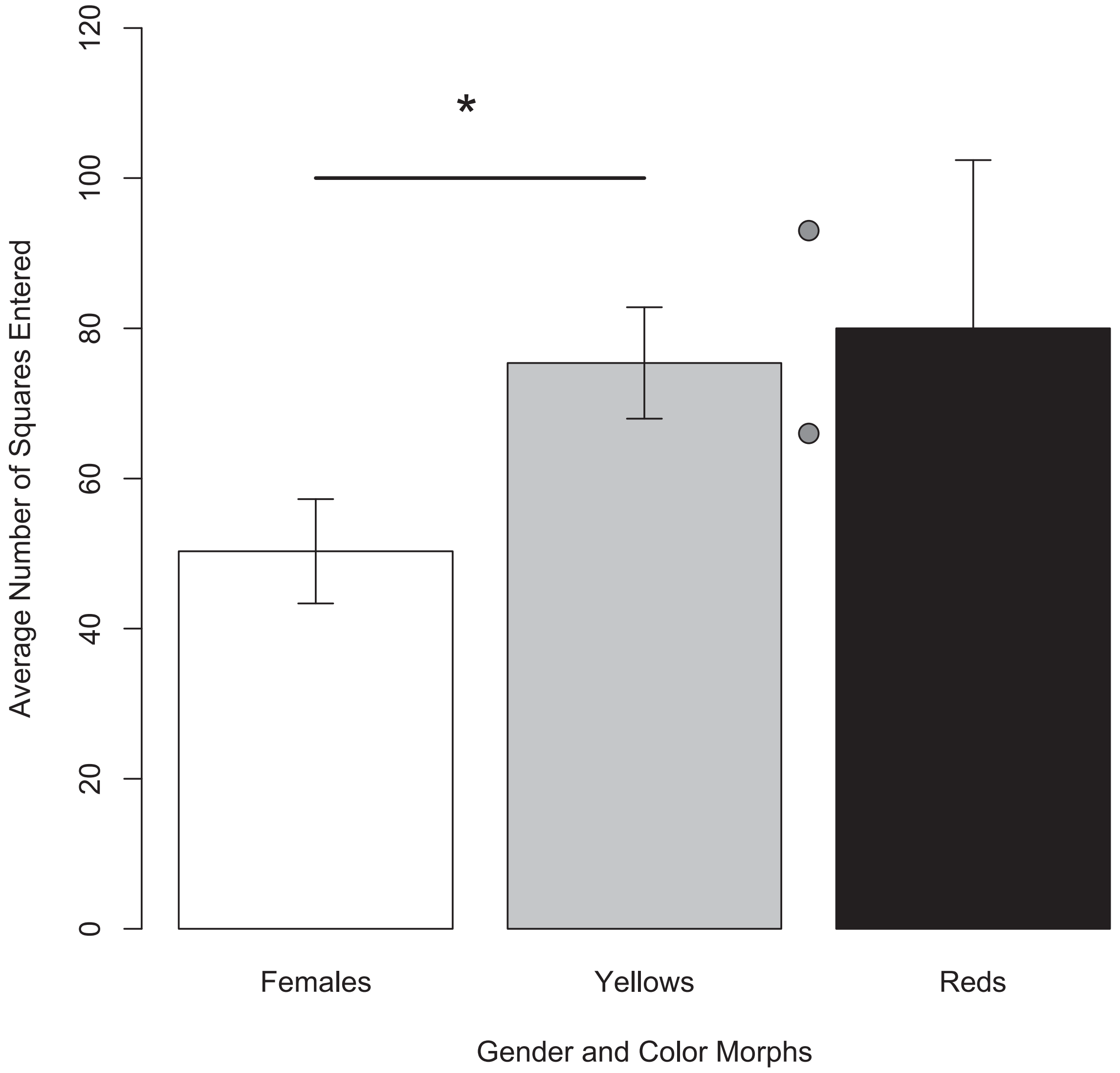

Figure 3. Female and male color morph activity level as measured by the average number of squares entered in the open field task. Average (±SEM) squares entered for females (white bar), yellow morphs (gray bar), and red morphs (black bar). Females and yellow males did differ significantly in the total number of squares explored ($p = 0.03$), while red males did not differ significantly from either of the other two groups.

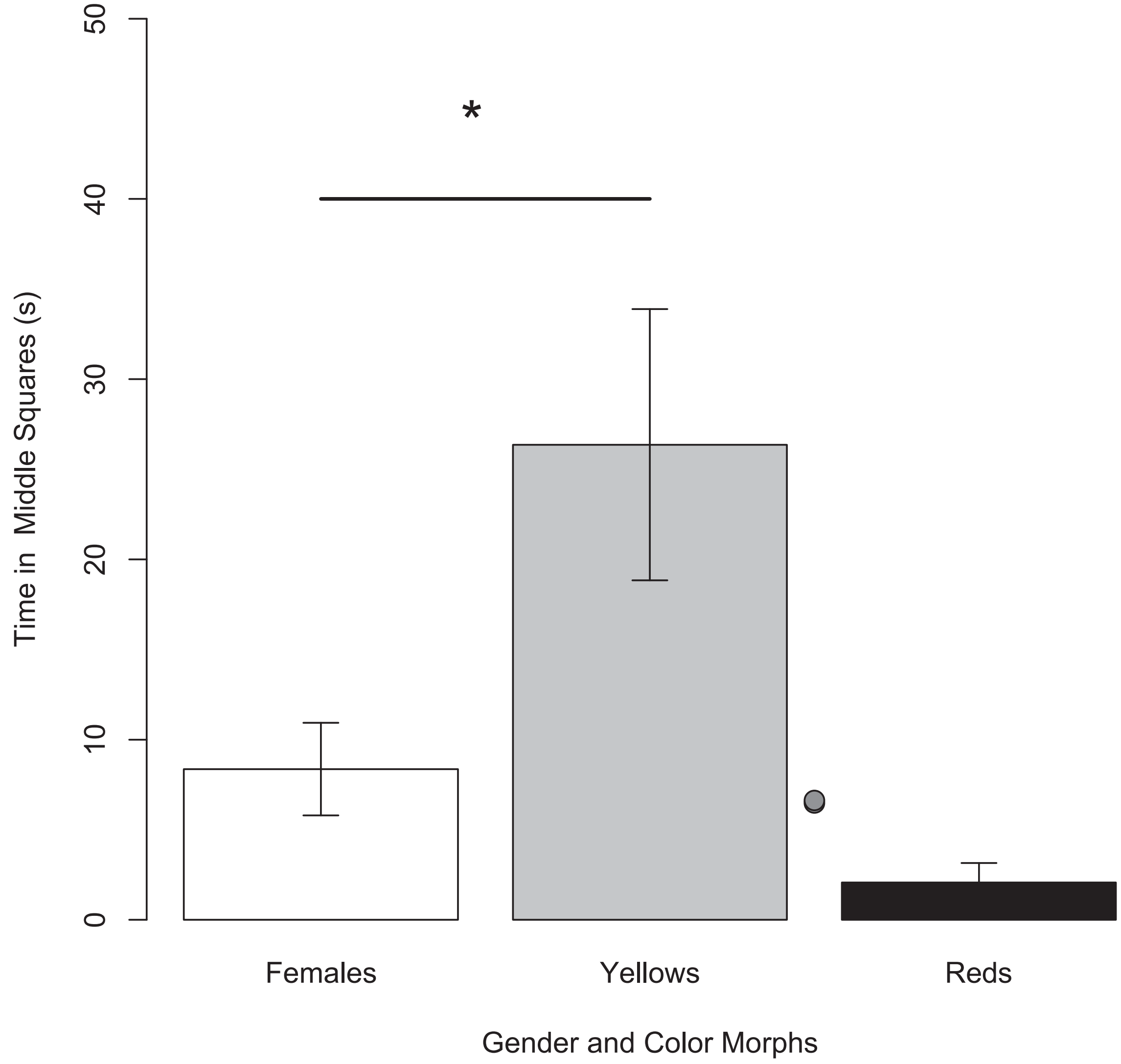

Figure 4. Female and male color morph duration of time spent in middle squares during the open field exploration task. Females and yellow males differed significantly in the time spent in middle squares ($p = 0.04$). Red males did not differ significantly from the other two groups in the duration of time spent in middle squares.

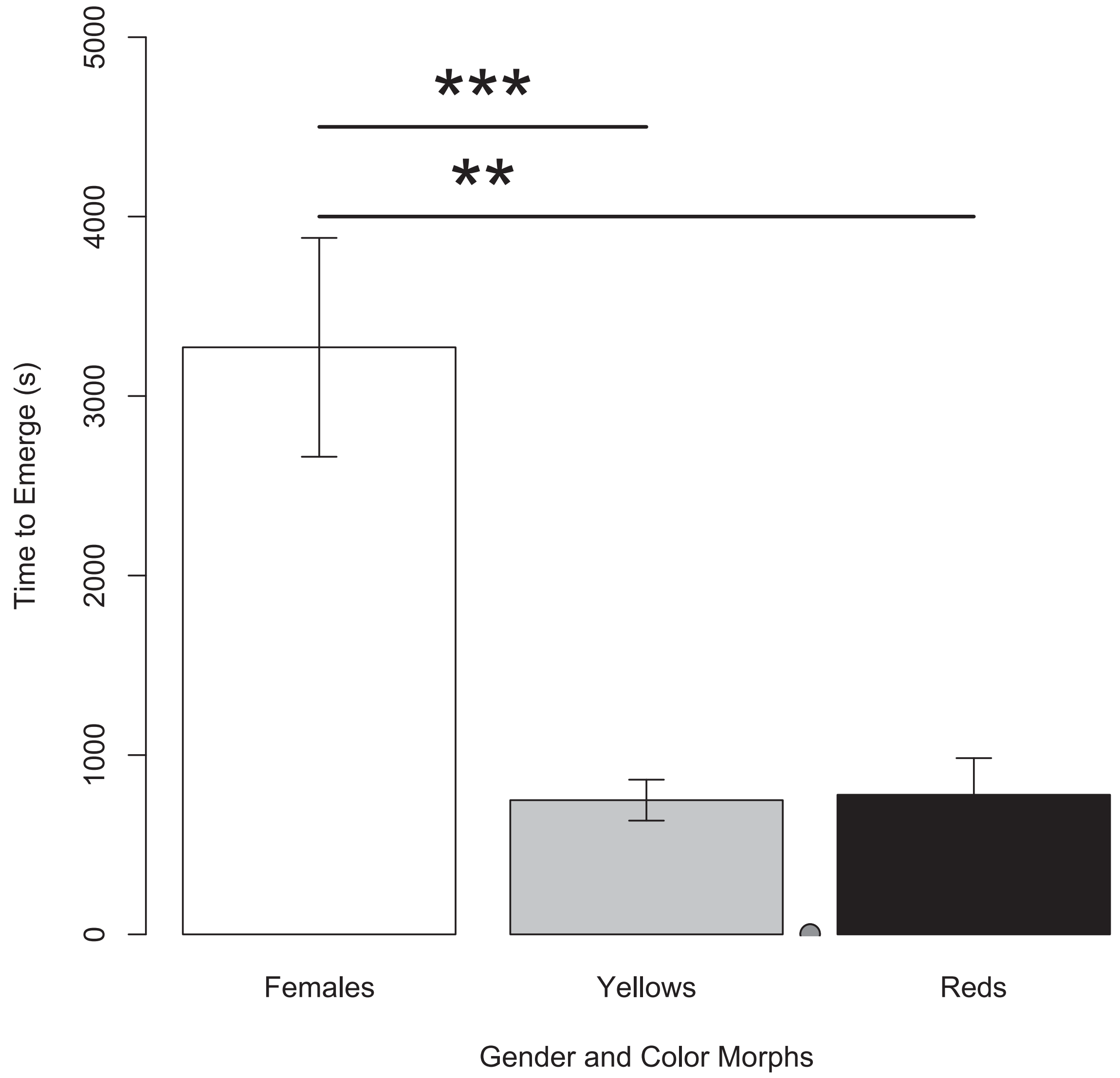

Figure 5. Female and male color morph times to emerge in the novel environment emergence task. Mean (± SEM) times to emerge action for females (white bar), yellow male morphs (gray bar), and red males (black bar). Females are significantly slower to emerge than either yellow ($p < 0.001$) or red males ($p = 0.002$).

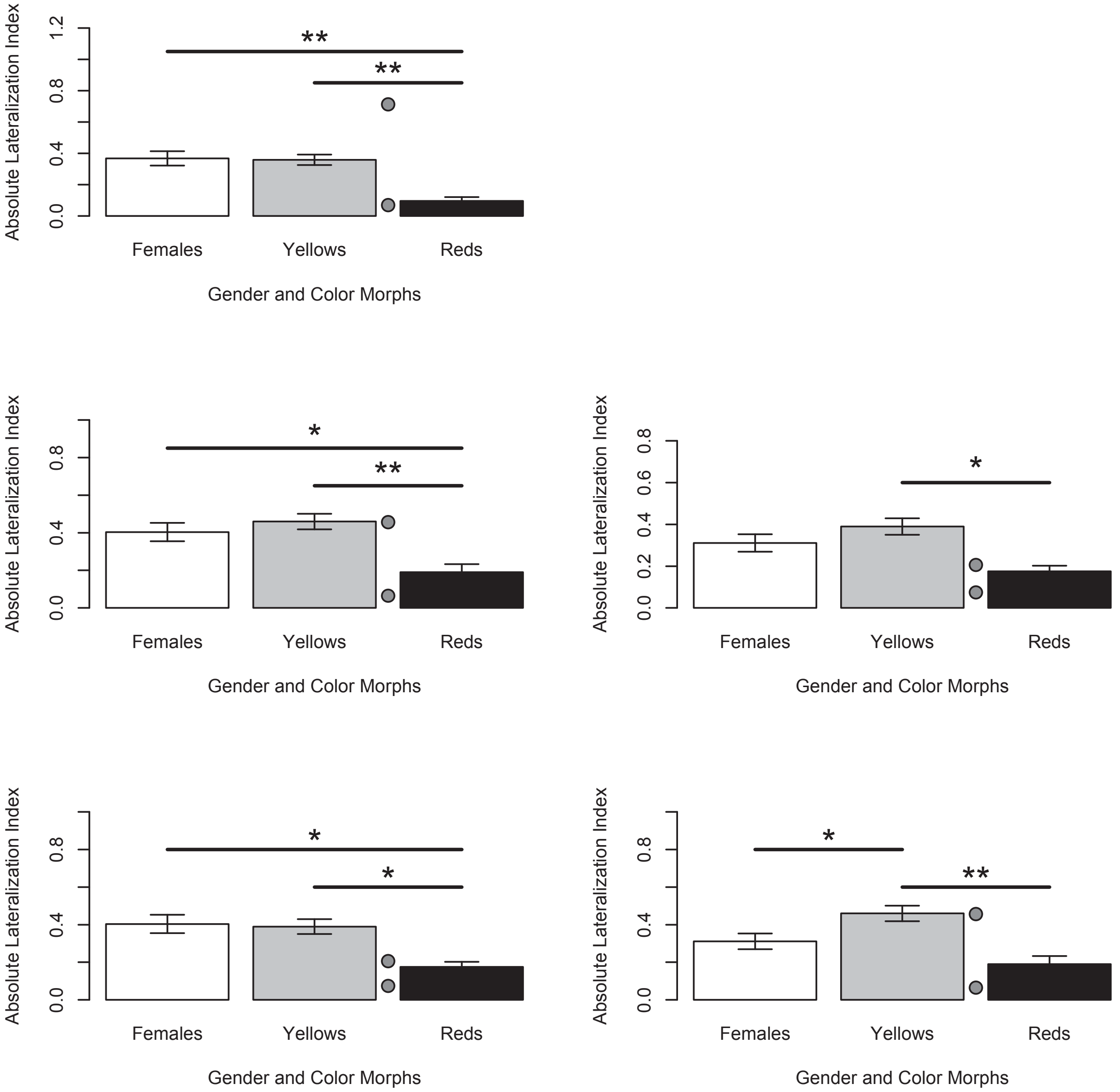

Figure 6. Female and male morph absolute lateralization indices (ALI) in the mirror octagon and circular lateralization tasks. Mean (±SEM) ALI scores for the mirror octagon (a), the circular lateralization task with male stimuli (b), the circular lateralization task with female stimuli (c), the circular lateralization task with opposite-sex stimulus fish (d), and the circular lateralization task with same-sex stimulus fish (e).

References

Ariyomo, T. O., & Watt, P. J. (2013). Aggression and sex differences in lateralization in the zebrafish. *Animal Behaviour*, *86*(3), 617–622. doi:10.1016/j.anbehav.2013.06.019

Arnott, G., Ashton, C., & Elwood, R. W. (2011). Lateralization of lateral displays in convict cichlids. *Biology Letters*, *7*(5), 683–5. doi:10.1098/rsbl.2011.0328

Bakker, T. (1985). Two-way selection for aggression in juvenile, female and male sticklebacks (Gasterosteus aculeatus L.), with some notes on hormonal factors. *Behaviour*, *93*(1), 69–81. doi:10.1163/156853986X00748

Bakker, T. (1986). Aggressiveness in sticklebacks (Gasterosteus aculeatus L.): a behaviour-genetic study. *Behaviour*, *98*(1), 1–114. doi:10.1163/156853986X00937

Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: a study with 16 species of fish. *Laterality*, *5*(3), 269–84. doi:10.1080/713754381

Bisazza, A., Rogers, L. J., & Vallortigara, G. (1998). The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neuroscience and Biobehavioral Reviews*, *22*(3), 411–26. doi:10.1016/S0149-7634(97)00050-X

Bottini, G., & Toraldo, A. (2003). The influence of contralesional targets on the cancellation of ipsilesional targets in unilateral neglect. *Brain and Cognition*, *53*(2), 117–120. doi:10.1016/S0278-2626(03)00091-5

Brown, C., & Braithwaite, V. A. (2004). Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. *Animal Behaviour*, *68*(6), 1325–1329. doi:10.1016/j.anbehav.2004.04.004

Brown, C., Burgess, F., & Braithwaite, V. A. (2007). Heritable and experiential effects on boldness in a tropical poeciliid. *Behavioral Ecology and Sociobiology*, *62*(2), 237–243. doi:10.1007/s00265-007-0458-3

Brown, C., Jones, F., & Braithwaite, V. (2005). In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, *70*(5), 1003–1009. doi:10.1016/j.anbehav.2004.12.022

Cantalupo, C., Bisazza, A., & Vallortigara, G. (1995). Lateralization of Predator-evasion Response in a Teleost Fish (*Girardinus falcatus*). *Neuropsychologia*, *33*(12), 1637–1646. doi:10.1016/0028-3932(95)00043-7

Chapman, B. B., Morrell, L. J., & Krause, J. (2010). Unpredictability in food supply during early life influences boldness in fish. *Behavioral Ecology*, *21*(3), 501–506. doi:10.1093/beheco/arq003

Coleman, K., & Wilson, D. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, *56*(4), 927–936. doi:10.1006/anbe.1998.0852

Dadda, M., Domenichini, A., Piffer, L., Argenton, F., & Bisazza, A. (2010). Early differences in epithalamic left-right asymmetry influence lateralization and personality of adult zebrafish. *Behavioural Brain Research*, *206*(2), 208–15. doi:10.1016/j.bbr.2009.09.019

Diekamp, B., Regolin, L., Güntürkün, O., & Vallortigara, G. (2005). A left-sided visuospatial bias in birds. *Current Biology*, *15*(10), 372–373. doi:http://dx.doi.org/10.1016/j.cub.2005.05.017

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *The Journal of Animal Ecology*, *76*(6), 1128–38. doi:10.1111/j.1365-2656.2007.01284.x

Enquist, M., & Jakobsson, S. (1986). Decision Making and Assessment in the Fighting Behaviour of Nannacara anomala (Cichlidae, Pisces). *Ethology*, *72*(2), 143–153. doi:10.1111/j.1439-0310.1986.tb00614.x

Earley, R., Hsu, Y., & Wolf, L. (2000). The use of standard aggression testing methods to predict combat behaviour and contest outcome in *Rivulus marmoratus* dyads (Teleostei: Cyprinodontidae). *Ethology*, *106*(8), 743–761. doi:10.1046/j.1439-0310.2000.00586.x

Espinoza, W. A. S. (2011). *Sexual differentiation, neurobiology, and behaviour in the convict cichlid (Cryptoheros nigrofasciatus).*

Facchin, L., Bisazza, A., & Vallortigara, G. (1999). What causes lateralization of detour behavior in fish? Evidence for asymmetries in eye use. *Behavioural Brain Research*, *103*(2), 229–34. doi:10.1016/S0166-4328(99)00043-1

Heiligenberg, W. (1965). Colour polymorphism in the males of an African cichlid fish. *Proceedings of the Zoological Society of London*, *146*(1), 95–97. doi:10.1111/j.1469-7998.1965.tb05202.x

Hurd, P. L. (2006). Resource holding potential, subjective resource value, and game theoretical models of aggressiveness signalling. *Journal of Theoretical Biology*, *241*(3), 639–48. doi:10.1016/j.jtbi.2006.01.001

Jakobsson, S., Radesäter, T., & Järvi, T. (1979). On the Fighting Behaviour of Nannacara anomala (Pisces, Cichlidae)♂♂. *Zeitschrift Für …*, *49*, 210–220. doi: 10.1111/j.1439-0310.1979.tb00288.x

Just, W., & Morris, M. R. (2003). The Napoleon Complex: why smaller males pick fights. *Evolutionary Ecology*, *17*(5/6), 509–522. doi:10.1023/B:EVEC.0000005629.54152.83

Larson, E. T., O'Malley, D. M., & Melloni, R. H. (2006). Aggression and vasotocin are associated with dominant-subordinate relationships in zebrafish. *Behavioural Brain Research*, *167*(1), 94–102. doi:10.1016/j.bbr.2005.08.020

Linke, H., & Staeck W. (1994) African Cichlids I Cichlids From West Africa: A handbook for their identification, care, and breeding. Melle, Germany: Tetra-Press.

Martin, E., & Taborsky, M. (1997). Alternative male mating tactics in a cichlid, Pelvicachromis pulcher : a comparison of reproductive effort and success. *Behavioral Ecology and Sociobiology*, *41*(5), 311–319. doi:10.1007/s002650050391

Moscicki, M. K., Reddon, A. R., & Hurd, P. L. (2011). Lateralized behaviour of a non-social cichlid fish (Amatitlania nigrofasciata) in a social and a non-social environment. *Behavioural Processes*, *88*(1), 27–32. doi:10.1016/j.beproc.2011.07.004

Nwadiaro, C. (1985). The distribution and food habits of the dwarf African cichlid, *Pelvicachromis pulcher* in the River Sombreiro, Nigeria. *Hydrobiologia*, *164*(121), 157–164. doi:10.1007/BF00008719

Ospina-Álvarez, N. & Piferrer, F. (2008). Temperature-Dependent Sex Determination in fish revisited: prevalence, a single sex ratio response patter, and possible effects of climate change. *PLoS ONE*, 3(7). doi: 10.1371/journal.pone.0002837

Reddon, A. R., & Balshine, S. (2010). Lateralization in response to social stimuli in a cooperatively breeding cichlid fish. *Behavioural Processes*, *85*(1), 68–71. doi:10.1016/j.beproc.2010.06.008

Reddon, A. R., & Hurd, P. L. (2008). Aggression, sex and individual differences in cerebral lateralization in a cichlid fish. *Biology Letters*, *4*(4), 338–40. doi:10.1098/rsbl.2008.0206

Reddon, A. R., & Hurd, P. L. (2009). Individual differences in cerebral lateralization are associated with shy–bold variation in the convict cichlid. *Animal Behaviour*, *77*(1), 189–193. doi:10.1016/j.anbehav.2008.09.026

Reddon, A. R., & Hurd, P. L. (2013). Water pH during early development influences sex ratio and male morph in a West African cichlid fish, Pelvicachromis pulcher. *Zoology (Jena, Germany)*, 1–5. doi:10.1016/j.zool.2012.11.001

Robins, A, Lippolis, G., Bisazza, A, Vallortigara, G., & Rogers, L. (1998). Lateralized agonistic responses and hindlimb use in toads. *Animal Behaviour*, *56*(4), 875–881. doi:10.1006/anbe.1998.0877

Römer, U., & Beisenherz W. (1996). Environmental determination of sex in *Apistogramma* (Chiclidae) and two other freshwater fishes (Teleostei). *Journal of Fish Biology*, *48*(4): 714-725. doi: 10.1111/j.1095-8649.1996.tb01467.x

Rubin, D. (1985). Effect of pH on sex ratio in cichlids and a poecilliid (Teleostei). *Copeia*, *1985*(1), 233–235. doi:10.2307/1444818

Scharnweber, K., Plath, M., & Tobler, M. (2011). Examination of boldness traits in sexual and asexual mollies (*Poecilia latipinna*, *P. formosa*). *Acta Ethologica*, *14*(2), 77–83. doi:10.1007/s10211-011-0097-6

Schwartzer, J. J., Ricci, L. A, & Melloni, R. H. (2013). Prior fighting experience increases aggression in Syrian hamsters: implications for a role of dopamine in the winner effect. *Aggressive Behavior*, *39*(4), 290–300. doi:10.1002/ab.21476

Snekser, J. L., & Itzkowitz, M. (2014). Contrasting Parental Tasks Influence Parental Roles for Paired and Single Biparental Cichlid Fish. *Ethology*, *120*(5), 483–491. doi:10.1111/eth.12221

Sovrano, V. a, Bisazza, A., & Vallortigara, G. (2001). Lateralization of response to social stimuli in fishes: a comparison between different methods and species. *Physiology & Behavior*, *74*(1-2), 237–44. doi:10.1016/S0031-9384(01)00552-2

Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A Methodological Review of Personality-Related Studies in Fish: Focus on the Shy-Bold Axis of Behavior. *International Journal of Comparative Psychology*, *23*(1), 1–25.

Uttl, B., & Pilkenton-Taylor, C. (2001). Letter Cancellation Performance Across the Adult Life Span. *The Clinical Neuropsychologist (Neuropsychology, Development and Cognition: Section D)*, *15*(4), 521–530. doi:10.1076/clin.15.4.521.1881

Vallortigara, G. (2000). Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. *Brain and Language*, *73*(2), 189–219. doi:10.1006/brln.2000.2303

Vallortigara, G. (2006). The evolutionary psychology of left and right: costs and benefits of lateralization. *Developmental Psychobiology*, *48*(6), 418–427. doi:10.1002/dev.20166

Vallortigara, G., Rogers, L., Bisazza, A., Lippolis, G., & Robins, A. (1998). Complementary right and left hemifield use for predatory and agonistic behaviour in toads. *Neuroreport*, *9*(14), 3341–3344. Retrieved from http://journals.lww.com/neuroreport/Abstract/1998/10050/Complementary_right_and_left_hemifield_use_for.35.aspx

Wong, M., & Balshine, S. (2011). Fight for your breeding right: hierarchy re-establishment predicts aggression in a social queue. *Biology Letters*, *7*(2), 190–3. doi:10.1098/rsbl.2010.0639

Supplemental

Rationale

Aggression

A mirror task is commonly used to measure aggressive responses to a mirror image; this method has been validated neurologically (Toms, Echevarria, & Jouandot, 2010). A study in which a serotonin inhibitor was administered to fire-mouth cichlids led to an increase in aggressive responses in the mirror image task (Adams, Liley, & Gorzalka, 1996). One of the reasons I chose the mirror task is because it automatically size matches the fish with their opponent and does not require additional fish for the test or repeated testing. Providing a standard opponent would have required providing each fish with a range of opponents since the behavior of the test subject is dependent on the behavior of their opponents (Franck & Ribowski, 1987). Additionally, it has been noted that the outcome of a recent fight impacts an individual's aggression in a variety of species including some fish (Hsu, Early, & Wolf, 2006) making it a further concern that providing standard opponents might change the behavior of the stimulus fish over repeated exposures. By avoiding using standardized opponents, and thus, leaving the focal animal to make the decision to escalate the encounter, and housing the fish in a home environment less exposed to dominance hierarchies or fighting that could result in wins or losses, I have neatly avoided the issue of how fighting experience could have impacted my results (see housing details).

Still, various experiments have quantified aggression by measuring different aspects of behavior in the mirror task. Some have used latency to the first aggressive act (e.g. Chang, Li, Early, & Hsu, 2012) while others measure aggression by bites or mean biting rates (Franck & Ribowski, 1987; Reddon & Hurd, 2013). To compound the issue, latency to attack a mirror image might be expected to correlate with boldness thus making it difficult to tease out what is due to aggression and what is due to boldness in such a situation. Even so, the relationship between boldness and aggression seems to be a meaningful one as being a bold and aggressive fish might be more rewarding with fish being able to carve out the better resource-based territories or be more discerning about mates.

Kribensis establish and defend territories, so it was necessary to give the fish an opportunity to establish a territory (24 hours) before testing them for aggression. Preliminary runs of fish the lab suggested that the 10 minute mirror exposure period of behavioral observation used in Reddon and Hurd (2008 and 2013) was not long enough to capture the aggressive action in Kribensis, as none of these preliminary subjects run using the Reddon and Hurd (2008) protocol time interacted with, or even seemed to notice, the mirror. Further testing revealed that an hour of exposure time was sufficient to elicit aggression in 40% (8 out of 20).

Boldness

A wide variety of tasks have been used to measure boldness in fish, from measuring responses to novel objects and novel environments, to responses to predation risk (Toms et al., 2010), among the most widely used is the emergence task (Brown & Braithwaite, 2004; Brown, Burgess & Braithwaite, 2007; Brown, Jones & Braithwaite, 2005). The best assay for boldness seems to depend upon the species being tested. For example in guppies (*Poecilia reticulata*), it seems that the open field and emergence tasks, which are correlated with each other, do measure boldness, while the novel object task does not (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). The experience with guppies differs significantly from that of the three-spined stickleback (*Gasterosteus aculeatus*) where scores from an open field task do correlate with scores from a task measuring the response to a novel object in a familiar environment (Dingemanse et al., 2007). However the open field task is widely recognized as a measure of boldness and it has been shown to correlate well with an emergence task in convict cichlids (Moscicki & Hurd, 2014).

The open field task provides a means of testing an animal's reactivity to a new and open-spaced area, which ought to be frightening to a lone animal (Champaign, Hoefnagels, de Kloet, & Richardson, 2010). In many animals, including fish, a large open space leads to wall hugging and following behavior, known as thigmotaxis, leading the animals avoid the open center areas, whether in their natural environments or in the labs (Champaign et al., 2010). It is believed that thigmotaxis is an evolved adaptive behavior that promotes finding means of escape or shelter (Champaign et al., 2010). Boldness can therefore be measured by the amount of time spent in middle squares: those away from the walls.

In addition to the variety of ways of measuring boldness, there are two of ways of providing open field-testing. The first entails introducing the animal to the task by force, whereby the animal is placed "in the environment with no opportunity to escape" (Carter et al. 2013, p. 468). The second provides the animal with the opportunity to explore the open field freely, by attaching to or placing the home environment into the open field (Carter et al., 2013).

In this experiment, I adopted the first method as moving the home environment into the testing arena was simply not feasible. However, the fish were given a week between each of the tests to allow them a chance to recover from any stresses of testing.

Since, as previously stated, tests of emergence and tests in an open field are correlated with one another in guppies (Burns, 2008; Carter et al., 2013) and additional evidence from our own lab (Mosiciski & Hurd, 2014) has shown similar correlations between an open field exploration test and a novel environment test in convict cichlids, I chose to use the emergence into a novel environment task as an additional test to measure the bold-shy axis as it is a classic measure of boldness and is widely used. The time from the door of the start box being opened to the time the fish leaves the safety of the start box is the measure of boldness in the fish.

Previous studies in our lab on different species have used a cut-off period of 10 minutes. Preliminary tests with this species demonstrated that very few of the fish would leave the start box within a 10-minute time frame. Increasing the cut off period to 20 minutes allowed us to observe more of the fish emerging time prior to the cut off. When it came time to actually run the fish, there was increased concern as many of the initial fish to be tested did not leave within the 20 minute cut-off. Due to concerns, I chose to repeat the test after a two-day break for a maximum of 10 tests or the fish emerged, whichever came first, and this managed to capture a majority of the fish while still enabling me to identify their level of boldness.

Lateralization

Cerebral lateralization, or simply lateralization, is easily measured in fishes through eye use. Since the eyes are laterally placed and the fields of vision hardly overlap (Northmore, 2011), it means that a majority of the information from one eye is sent to the opposite hemisphere of the brain (Northmore, 2011; Reddon & Hurd, 2009; Facchin, Bisazza, & Vallortigara, 1999). There are a variety of methods one can use to measure lateralization depending on the type of context provided to the subject.

The quasi-circular mirror lateralization task, or octagonal mirror task, was chosen as the method of assessing behavioral lateralization as it provides a less variable method of assessing lateralization than the more common detour task. The advantages of the quasi-circular mirror lateralization task are that the experiences of the fish are generally quite standard as the experimenter is blocked from view and this method would provide a perceived social environment where the “stimulus” is size matched as it is the experimental fish’s own image.

Additionally, there were concerns due to all the preliminary testing results in the other apparatuses that the fish would be less than cooperative in the detour task under such testing conditions.

Preliminary tests in the octagonal mirror task revealed similar difficulties to the emergence into a novel environment as none of the fish would leave the central starting chamber within the allotted 10-minute time frame. Repeated testing did not improve the situation. The resultant decision was to move to a method of release that would force the fish to participate in the task, so I adopted the method of release used in the open field task.

With the evidence of differences in lateralization on the basis of context in poeciliid fish (*Gamusia holbrooki* & *Girardinus falcatus*; Bisazza, Facchin, Pignatti & Vallortigara, 1998) and the evidence from Brown, Gardner, and Braithwaite (2004) that two populations within a single species can differ with respect to both personality and lateralization I chose to address the question: how might different stimuli cause variation in the lateralization of the identified groups of kribensis?

I decided to test the fish in a lateralization task designed in our lab that would allow us to present the fish with specific stimuli, in this case groups of three males or females. The benefits of testing the fish in both this task and in the octagonal mirror task was threefold: 1) it allowed me to check if the fish are simply swimming in a particular direction around in the apparatus (clockwise vs. counterclockwise), 2) it enabled me to test how the fish would be lateralized if viewing the opposite sex, and 3) it permitted me to explore how live stimulus fish differ from the perceived social stimulus of the octagonal mirror task.

Additional Data Analysis

Type three ANOVAS and ANCOVAs were used to determine if any relationships existed between any of the outcome measures in all of the tasks. Type three is more robust as it has the ability to detect both main and interaction effects simultaneously, however, its power to detect a main effect is slightly reduced. If an ANOVA returned a significant relationship I conducted post-hoc tests using the R function pairwise.t.test(). Principle component analyses (using the princomp() command in R) were used to identify meaningful components and outcome measures in the mirror aggression, open field exploration tasks, and then to identify the outcome measures that best represented the data as a whole. Multidimensional scaling (using the cmdscale()

command in R) was used to identify graphically if there were any overall explanations for the data.

Additional Results

Comparisons between tasks

Given that personality is defined as traits that are consistent across time and events, I had reasons to expect that the two measures of boldness would be related to one another and that the lateralization indices from the two tests would relate. For these tests the LI measures were compared to LIs and the ALI measures to ALIs. Additionally, because of the crossover of sexes in the same-sex and opposite-sex stimuli categories the tests of the circular lateralization were just tested against its counterpart (i.e., males against females and same sex against opposite sex). Otherwise the single sex stimuli fish categories would have been highly related to the mixed sex categories, since one or two of the groups would have contained the values from that single sex category.

I also had *a priori* reasons to suspect that aggression might interact with boldness (Brown & Irving, 2014) and with lateralization (Reddon & Hurd, 2008). I ran ANCOVAs to determine if there were any main, or interaction effects, for five aggression outcomes (time to first aggressive action, number of charges, number of tail beats, time spent tail beating, and whether the fish behaved aggressively in the mirror aggression test) with the sex or male morphs and any of my other outcome measures of interest. Finally, lateralization is also thought to correlate with the bold-shy axis (Reddon & Hurd, 2009) so I tested the shy-bold behavioral outcomes against each of the lateralization indices (LI and ALI).

Comparison Between Boldness Measures

Results

For both females and male morphs the smaller the log time to emerge corresponds with a larger number of total squares entered, however, the steepness of the slopes of each group tends to differ from each other, with females having the most horizontal slope and red males having the closest to 45° slope ($p = 0.07$). There was an overall trend of lower log emerge times for fish spending more time in middle squares ($p = 0.08$). For males, the more time spent in middle squares the more quickly they emerged (negative correlation), while females who spent more time in middle squares emerged more slowly (positive correlation; $p < 0.001$, Table S.2). Finally, fish that entered more squares during "the freak-out period" also tended to have larger log emerge times ($p = 0.07$).

Discussion

The only significant relationship between the outcome measures of my two boldness tasks (the open field and the novel environment emergence tasks) appeared in the interaction between the time spent in middle squares and the sex and color morph on the log transform of the time to emerge. Males of both color types demonstrated a negative correlation; in that the more time they spent in middle squares the more quickly they emerged in the novel environment emergence task (Figure S.4). Females, conversely, emerged more slowly if they spent more time in the middle squares. This result is the reverse of what I expected. A few individuals could be the cause of the unexpected behavior of the females; however, this could also be explained by a difference in activity level. Males in general seem to be higher in activity as they entered more squares on average than females (Figure 3a). An alternative explanation is that there may be differences between the sexes based on coping style. Males could have a more active coping style and would therefore want to move more quickly to get out of a potentially dangerous situation (being in middle squares). Females, on the other hand, could follow more of a reactive coping style and move more slowly in and through the dangerous middle squares so as to prevent being identified by a potential predator.

Comparisons Between Lateralization Indices

Results

No significant main or interaction effects were found between the LI from the mirror octagon and sex/color morph and the LI in the circular lateralization task with male stimuli, females, when the stimulus fish were of the same, or opposite sex (Table S.3). There was no significant main effect or interaction effects of ALI from the mirror octagon and sex/color morph on ALI scores in the circular lateralization task, with stimulus either males or with fish of the opposite sex (Table S.3). There was, however, a significant and positive main effect of ALI from the mirror octagon with respect to the ALI with female stimuli as higher ALI scores in the mirror octagon matched up with higher ALI scores with female stimuli ($p = 0.04$, Table S.3). A higher

ALI score in the mirror octagon also tended to correspond to a higher ALI in the circular lateralization task with stimulus fish of the same sex (*p* = 0.053, Table S.3).

There was no significant main effect or interaction effect of the LI with male stimuli on LI with female stimuli, but a higher ALI with male stimuli in the circular lateralization did relate to higher ALI scores with female stimuli (*p* = 0.02, Table S.3). No significant main or interaction effects of LI with stimulus fish of the same sex were seen on LI with stimulus effects of the opposite sex, but higher ALI scores in the circular lateralization task with stimulus fish of the same sex also coincide with higher ALI scores for stimulus fish of the opposite sex (*p* = 0.01, Table S.3).

Discussion

A comparison between the lateralization indices and absolute lateralization indices of the different lateralization tasks revealed only three relationships. First, the ALI in the mirror octagon had a moderately strong positive relationship with the ALI with female stimulus fish in the circular lateralization task (Figure S.5). The ALI scores in the mirror octagon task corresponded to similarly high or higher ALI scores for the circular lateralization task with female stimuli, which indicates that fish display similar strengths of lateralization in the two tasks. Secondly, the ALI scores from the circular lateralization task with male stimuli had a moderately strong positive relationship with the ALI with female stimulus fish (Figure S.6). Finally, the ALI scores from viewing fish of the same sex also shared a moderately strong positive relationship with ALI from viewing fish of the opposite sex (Figure S.7). These last two pairs of relationships suggest that in the circular lateralization task fish display similar strengths of lateralization regardless of the sex of the stimuli. It is interesting to note that the ALI from the mirror octagon did not appear to share a relationship with any of these three other conditions in the circular lateralization task and LI did not appear to be related between either of the tasks or conditions.

Comparison Between Aggression and Boldness

Results

For female and red males the greater number of lateral displays performed the more time they spent "freaking-out" during the open field task, however, yellow males exhibited a reversed pattern of behavior and spent less time “freaking-out” the more lateral displays they had performed ($p = 0.045$, Table S.4). All of the other aggression measures had non-significant main and interaction effects on time spent “freaking-out” or the number of squares entered during “the freak-out period” (Table S.4).

I did not find a significant main effect of time to first aggressive action or interaction effect with sex and color morph on the total number of squares entered in the open field ($p = 0.99$ and $p = 0.37$ respectively, Table S.4). This result suggests that fish have similar activity levels in the open field task and that time to first aggressive action and sex/color morph has no effect on the behavior in the open field task. Number of charges and time spent charging did have significant interaction effects with sex and color morph on the total number of squares entered ($p = 0.01$ for both cases, Table S.4), but no main effects (Table S.4). Males of both color types demonstrated a positive correlation, in that the more charges they engaged in or the more time they spent charging the more squares they entered in the open field task. Females, conversely, entered fewer squares the more charges or the more time they spent engaging in charges. Time spent performing lateral displays trended towards significance as an interaction effect with sex and color morph on the total number of squares entered ($p = 0.053$, Table S.4). None of the other aggressive behaviors had significant main or interaction effects on total number of squares entered (Table S.4).

The proportion of corner squares entered was entirely unrelated to any of the aggressive behaviors, since no main and interaction effects were significant (Table S.4). The time to first aggressive action was significantly related as both main and interaction effects on the proportion of edge squares entered ($p = 0.01$ and $p = 0.046$ respectively, Table S.4). Females and red males exhibited a slight negative relationship between time to first aggressive action and the proportion of edge squares entered which matched the overall pattern of behavior, while yellow males demonstrated a slight positive relationship. The number of bites was also positively related to the proportion of edge squares entered as a main effect ($p = 0.003$, Table S.4), but was not significant as an interaction with sex and color morph ($p = 0.12$, Table S.4). Whether a fish was aggressive or not had both significant main effects and interaction effects on the proportion of edge squares entered ($p < 0.001$ and $p = 0.003$ respectively, Table S.4). Aggressive females entered a greater proportion of edge squares than non-aggressive females ($p = 0.003$) and non-aggressive yellow males entered a greater proportion of edge squares than aggressive yellow males ($p = 0.24$). Red males entered approximately the same proportion of edge squares regardless of their aggressive status ($p = 0.99$). The number of lateral displays trended towards significance as sharing a positive relationship with the proportion of edge squares entered ($p = 0.09$, Table S.4), the larger the proportion of edge squares entered coincided with a greater number of lateral displays performed. The larger proportion of edge squares entered also corresponded with a larger number of lateral displays performed ($p = 0.01$, Table S.4); all other main and interaction effects on the proportion of edge squares entered were non-significant (Table S.4).

Time to first aggressive action and number of bites performed both had a significant main effects on the proportion of middle squares entered ($p = 0.04$ and $p = 0.03$ respectively, Table S.4), but neither had significant interaction effects with sex and color morph (Table S.4). Time to first aggressive action was positively related to the proportion of middle squares entered while number of bites was negatively related to the proportion of middle squares entered. Whether a fish was aggressive or not had both significant main and interaction effects on the proportion of middle squares entered ($p = 0.006$ and $p = 0.03$ respectively, Table S.4). Non-aggressive females entered a significantly greater proportion of middle squares than their aggressive counterparts ($p = 0.03$). Although not significant, aggressive males entered a greater proportion of middle squares than non-aggressive ones (red males: $p = 0.30$ and yellow males: $p = 0.44$). The number of lateral displays and time spent performing bites both tended to be negatively related to the proportion of middle squares entered ($p = 0.08$ and $p = 0.06$ respectively, Table S.4), All other aggressive behaviors had non-significant main and interaction effects on the proportion of middle squares entered (Table S.4).

The time to first aggressive action had a significant and positive main effect (but not an interaction effect) on the time spent in corner squares ($p = 0.004$, Table S.4). Whether the fish was aggressive or not had both significant main effects and interaction effects on the time spent in corner squares ($p < 0.001$ and $p = 0.009$ respectively, Table S.4). Non-aggressive females spent significantly more time in corner squares than their aggressive counterparts ($p < 0.001$). Non-aggressive red males also spent more time in corner squares (but not significantly, $p = 0.52$) and aggressive yellow males spent slightly more time in corner squares than non-aggressive yellow males ($p = 0.75$). The number of bites and time spent performing bites had a negative relationship with the time spent in corner squares ($p < 0.001$ and $p < 0.001$ respectively, Table

S.4). Females and red males displayed negative relationships between either the number of bites and duration of bites and the time spent in corner squares, while yellow males showed slightly positive correlations between the same pairs of behaviors ($p = 0.01$ and $p = 0.02$ respectively). Females and red males exhibited negative relationships between time to first aggressive action and the time spent in corner squares, while yellow males demonstrated a slight positive relationship. The number of charges and number of lateral displays both had negative relationships trending towards significance with the time spent in corner squares ($p = 0.06$ for each, Table S.4). The time to first aggressive action shared a slight negative relationship with the time spent in edge squares ($p = 0.002$, Table S.4). Females and red males exhibited negative relationships between time to first aggressive action and the time spent in edge squares, while yellow males demonstrated a slight positive relationship ($p = 0.01$, Table S.4). Aggressive females spent significantly more time in edge squares than their non-aggressive counterparts ($p < 0.001$). Aggressive red males also spent more time in edge squares (but not significantly, $p = 0.52$) and aggressive yellow males tended to spend less time in edge squares than non-aggressive yellow males ($p = 0.08$). The number of bites and time spent performing bites both had significant main and interaction effects on the time spent in edge squares (all $p < 0.001$, Table S.4). Females and red males followed the overall behavior pattern and exhibited positive relationships between number or time spent performing bites and the time spent in edge squares, while yellow males demonstrated a negative relationship. None of the other aggressive behaviors had any significant main or interaction effects on the time spent in edge squares (Table S.4) and all of the aggressive behaviors were non-significant as main or interaction effects on the time spent in middle squares (Table S.4).

Time to first aggressive action had a significant and positive main effect on the log time to emerge into a novel environment ($p = 0.01$, Table S.4) with females and yellow males following the behavior pattern while red males showed the reverse relationship ($p = 0.07$, Table S.4). This result appears to be based on whether or not the fish attacked the mirror, since the significant main effect disappears when the fish that never attacked the mirror are removed ($p = 0.91$). Non-aggressive females took significantly more time to emerge into the novel environment than their aggressive counterparts ($p = 0.03$). Aggressive red morph took more time to emerge (but not significantly, $p = 0.19$) and yellow males took similar amounts of time to emerge regardless of aggressive status (*p* = 0.63; overall *p* = 0.03 for the interaction term, Table S.4).

Analyses revealed a significant and negative main effect for the number of bites on the log time to emerge (*p* = 0.048, Table S.4). There were no significant main or interaction effects for the number of charges, number of lateral displays, or number of tail beats with sex and color morph on the log transformed time to emerge (Table S.4). Time spent performing bites had a significant negative main effect on the log time to emerge (*p* = 0.004, Table S.4); however, the interaction was not significant (Table S.4). There was a negative trend between the main effect of time spent performing charges and the log time to emerge (*p* = 0.06, Table S.4).

Discussion

My comparison between the aggressive outcome measures and the boldness measures reveals a complex relationship between aggression and boldness. First, in the open field task the time spent “freaking-out” only related to the number of lateral displays performed in the mirror aggression task. The number of lateral displays shares a very weak positive relationship with time spent “freaking-out” (Figure S.8). The yellow males have a slightly weak negative relationship between the number of lateral displays and the time spent “freaking-out,” where the more lateral displays performed the less time the fish spent “freaking-out.” The females demonstrate a moderately positive relationship and the red males show a strong positive relationship between the number of lateral displays and the time spent “freaking-out.” While this set of relationships could be driven by a few outliers or a common underlying trait, there are other possible explanations for why the fish would behave in this way. In the females and red males, this positive relationship may suggest that lateral displays are, to a certain degree, actually a measure of a “freak-out” – whereby the fish is reacting negatively to the mirror intruder and thus swimming back and forth with fins extended in a more panicked display to get the intruder to leave. Although, it is worth reiterating the fact that red males performed very few lateral displays compared to the yellow males and females. The negative relationship in the yellow males may instead indicate an active coping mechanism, where the fish is engaging in lateral displaying as a primary means of discouraging an intruder.

The total number of squares entered in the open field task related to both the number of charges and the time spent performing charges (Figure S.9 and Figure S.10). Females had a slightly negative relationship, yellow males a weakly positive relationship, and red males had a strong positive relationship for both relationships. This could be explained by the preferred division of labor based on sex roles in the fishes' natural history. The greater number and duration of charges and higher activity levels of the males would be more suitable for territory guarding and patrolling activities while the more stationary and high number and durations of charges would be best explained by stationary females guarding nest sites or fry (Snesker & Itzkowitz, 2014).

Time to first aggressive action in general weakly and negatively related to the proportion of edge squares entered (Figure S.11); however, the sex and color morphs did demonstrate differences in this relationship. Females followed the overall pattern and the relationship was weakly negative, red males expressed a weak relationship of an indeterminate nature, while yellow males ran counter to the general trend and had a weakly positive relationship (Figure S.11). Whether the fish was aggressive or not also shared a relationship with the proportion of edge squares entered. Aggressive females entered a significantly greater proportion of edge squares than their non-aggressive counterpart (Figure S.12). Number of bites also shared a weakly positive relationship with proportion of edge squares entered (Figure S.13). Time to first aggressive action shared a very weak positive relationship with the proportion of middle squares entered. This last result appears to be driven by the yellow males (Figure S.14). The number of bites had a weak negative relationship with the proportion of middle squares entered (Figure S.15). The more bites the fish performed the lower the proportion of middle squares the fish enters. The proportion of middle squares visited also shared a relationship with whether the fish was aggressive or not (Figure S.16). This relationship seems to be mainly driven by the females as they were the only group to differ significantly between the non-aggressive and aggressive interaction. It is, however, interesting to note that the non-aggressive females entered a larger proportion of middle squares than did either of the male morphs, while aggressive male morphs entered a larger proportion of middle squares than the aggressive females. These relationships with the proportion of squares entered run counter to all my expectations, that more aggressive fish would be more bold, as many of these relationships seem to suggest that non-aggressive fish are more bold. The non-aggressive females appear to be the cause of these counter intuitive behaviors.

The time to first aggressive action had a significant and slightly positive relationship with the time spent in corner squares (Figure S.17). The longer the fish took to perform an aggressive action the more time they spent in corner squares. This relationship suggests that fish with higher times to first aggressive action will be more shy (by spending more time in corner squares).

Whether a fish was aggressive or not was also related to the time spent in corner squares, non-aggressive females spent more time in corner squares than aggressive females (Figure S.18). Non-aggressive red males likewise had a higher mean time spent in corner squares than aggressive red males. Yellow males, on the other hand, were more evenly split in their average time spent in corner squares, although the non-aggressive ones did have a slightly lower mean. This suggests that non-aggressive females and (possibly) red males are also more shy fish than their aggressive counterparts, yellow males are not particularly more or less bold regardless of whether they are aggressive or not.

The number of bites and time spent performing bites were likewise related to the time spent in corner squares (Figure S.19 and Figure S.20). Females exhibited a strongly negative relationship between the number of, and time spent performing, bites and the time spent in corner squares. Red males, similarly, exhibited a moderate negative relationship between the two pairs of behavioral outcomes. Yellow males on the other hand exhibited a slight positive relationship between the number and time spent performing bites and the time spent in corner squares.

The time to first aggressive action generally shared a slight negative relationship with the time spent in edge squares; however, yellow males have a slight positive relationship between the two behavioral outcome measures (Figure S.21). Whether the fish was aggressive or not also related to the time spent in edge squares (Figure S.22). Aggressive females and red males spent, on average, more time in edge squares than their non-aggressive counterparts. Conversely yellow males spent more time in edge squares if they were non-aggressive. The number of and time spent performing bites also generally shared positive relationships with the time spent in edge squares (Figure S.23 and Figure S.24). Yellow males, however, continue to have inverse relationships when compared to females or red males as they showed a moderate negative relationship between the pairs of behavioral outcome measures.

Time to first aggressive action also had a positive relationship with the log time to emerge from the novel environment; however red males showed a slight negative relationship (Figure S.25). The log-transformed time to emerge in the novel environment emergence task and the interaction of sex and color morph on whether the fish was aggressive or not also shared a relationship. Non-aggressive females had a higher log emerge time than the aggressive females, yellow males appeared to have similar log emerge times regardless of their aggressive status, and aggressive red males had a higher average log emerge time than their non-aggressive counterpart (Figure S.26). The number of, and time spent performing, bites also shared moderate negative relationships with the log emerge time (Figure S.27 and Figure S.28).

The interaction of aggression and boldness measures paint a complex picture, as several results could be interpreted as both shy and bold. I will begin by discussing the stronger relationships which are based on whether the fish is aggressive or not. The proportion of middle and edge squares entered as a function of whether the fish is aggressive or not yields an unclear set of relationships. The males pattern of behavior, with non-aggressive fish entering a higher or the same proportion of edge squares and a lower proportion of middle squares, follows my expectations that less aggressive fish would be more shy. Females run counter to this expectation with non-aggressive fish entering a lower proportion of edge squares and a higher proportion of middle squares.

Time spent in corner and edge squares can be viewed as a measure of more and less shy. By spending more time in corner squares and less time in edge squares, as the non-aggressive females do, suggests that these are the most shy fish (as compared to their aggressive counterparts). Whereas, non-aggressive yellow males who spend more time in edge squares and an approximately equal amount of time in corner squares when compared to the aggressive yellow males are less shy and the aggressive ones could possibly be considered bold. Red males are more similar to the females in that they are more and less shy depending on whether they are non-aggressive or aggressive.

Perhaps the females’ pattern of behavior relative to the proportion of edge and middle squares is better explained by their pattern of behavior related to the time spent in corner and edge squares. The non-aggressive females spend more time in corner squares and less time in edge squares, have a higher proportion of middle squares entered and a lower proportion of edge squares entered. Perhaps these non-aggressive females are entering and leaving the corner squares via the middle squares rather than edge squares which would account for a higher proportion of middle squares entered. The aggressive females could instead be swimming around through the edge squares in more of a patrolling behavior which would help explain the lower proportion of middle squares entered.

Time to first aggressive action shares a similarly complex pattern of behavior. It is related to a larger proportion of middle squares entered, a lower proportion of edge squares entered and to less time spent in edge squares (which is indicative of more bold fish) but is also related to more time spent in corner squares and a longer log time to emerge (which is indicative of more shy fish). The non-aggressive females appear to be heavily driving the negative relationship between the time to first aggressive action and the proportion of edge squares entered as well as the positive relationship with proportion of middle squares entered. If aggressive females are performing more patrolling behaviors and non-aggressive females are swimming into middle squares and back into corner squares then that accounts for the deviation in those measures of boldness (proportion of middle and edge squares). The remainder of the relationships follow the expected pattern that less aggressive (or non-aggressive fish) are more shy than their aggressive counterparts.

The greater number of bites and greater time spent performing bites generally relates to a bolder fish as they seem to spend less time in corner and edge squares and have a faster log emerge time. However, four relationships in the results go against these general trends: females and red males spend a greater amount of time in edge squares as the number of bites or time spent performing bites increases; yellow males spend more time in corner squares; and the greater the number of bites performed the lower the proportion of middle squares entered. The increased time in edge squares and the lower proportion of middle squares entered can be explained by the possibility that bolder fish are actually spending more time patrolling or exploring the borders of the open field environment and so are not really behaving in a shy manner. The larger number and duration of bites relating to more time in corner squares for yellow males could potentially be explained as a defensive mechanism. If, as I believe, yellow males are less likely to be the dominant males in a tank of fish including red males, then they may swim to a safer section of the tank to evaluate the situation before they perform any other actions.

Comparison Between Aggression and Lateralization

Results

Time to first aggressive action was revealed to only trend towards a significant negative relationship with respect to LI in the mirror octagon task ($p = 0.09$, Table S.5), and there were no significant main effects or interaction effects on any of the other LI or ALI measures (Table S.5). The lateralization index (LI) from the mirror octagon task was significantly associated with whether the fish behaved aggressively in the mirror aggression test, non-aggressive fish exhibited a left eye bias, while aggressive fish were rather unbiased. There was no significant interaction between sex and color morph and fish aggression (Aggression: $p = 0.01$; Interaction: $p = 0.31$ respectively, Table S.5). No main or interaction effects occurred with respect to any of the ALI measures (mirror octagon or four circular lateralization variants) nor with respect to any of the circular lateralization LI variants (Table S.5).

The number of bites, charges, and lateral displays also had no significant main effects or interaction effects with respect to any of the LI or ALI measures (Table S.5). The number of tail beats had no significant main or interaction effects on LI or ALI in the mirror octagon task (Table S.5). However, the number of tail beats did have a number of main and interaction effects that trended towards significance with LI and ALI measures. The more tail beats attacks a fish performed corresponded with more right eye use for examining either male or female stimuli fish in the circular lateralization task (Male stimulus: $p = 0.09$; Female stimulus: $p = 0.06$, Table S.5). The strength of the lateralization (ALI) when viewing male stimuli fish in the circular lateralization task was higher in females that performed more tail beats, but lower in males of both morph types ($p = 0.10$, Table S.5). The ALI when viewing female stimuli fish was generally lower the more tail beats the fish performed, however, it was higher in females and in red males that performed more tail beats, while it was lower in yellow males who performed more tail beats (Main: $p = 0.08$; Interaction: $p = 0.06$, Table S.5). The ALI score when viewing fish of the same sex was generally lower in fish that performed more tail beats, both male morphs followed this trend, but females who performed more tail beats instead had higher ALI scores (Main: $p = 0.09$; Interaction: $p = 0.0501$; Table S.5). The overall trend when viewing fish of the opposite sex was that of lower ALI scores paired with more tail beats, yellow males followed the pattern, but females and red male morphs had higher ALI scores when they also had a higher number of tail beats (Main: $p = 0.07$; Interaction: $p = 0.10$, Table S.5).

The time spent performing bites, charges and lateral displays were not associated with any of the LI or ALI scores. Time spent performing lateral displays was somewhat negatively related to both the LI in the circular lateralization task when the stimuli fish were males ($p = 0.09$, Table S.5) and when the stimuli were of the opposite sex ($p = 0.07$, Table S.5). The relationship between time spent performing lateral displays and the two LI scores does however appear to be heavily driven by a few fish. The longer a fish spent tail beating corresponded with more right eye use for examining any stimuli in the circular lateralization task (Male stimulus: $p = 0.08$; Female stimulus: $p = 0.07$; Same-sex: $p = 0.10$; Opposite sex: $p = 0.053$, Table S.5). Females and red males that spent more time performing more tail beats were also more strongly lateralized when examining the female or same-sex stimuli fish while yellow males that spent longer performing tail beats were less strongly lateralized when viewing either the female or same-sex stimuli fish in the circular lateralization task (Female stimulus: $p = 0.09$; Same-sex: $p = 0.06$, Table S.5). All other main and interaction effects were non-significant with respect to the time spent tail beating (Table S.5).

Discussion

My comparison of aggression and lateralization measures only revealed one relationship significant at the $p = 0.05$ level, between whether a fish was aggressive or not and the LI from the mirror octagon. Non-aggressive fish appear to be lateralized towards a left eye bias while aggressive fish are rather neutral (Figure S.29). This relationship appears to be heavily driven by the non-aggressive females as both male morph types do not differ from 0 (meaning no eye preference and thus equal favoring of both eyes). None of the other LI or ALI measures showed any definitive relationship with any of the aggression measures.

Comparisons Between Boldness and Lateralization

Results

Time spent "freaking-out" in the open field task was positively associated with ALI in the mirror octagon ($p = 0.045$, Table S.6). Females and yellow males had positive relationships between the log transformed time to emerge in the novel environment emergence task and ALI with female stimuli, while red males had negative relationships between the two variables (Females: $p = 0.10$; Table S.6). Females and red males exhibited negative relationships between the log time to emerge and the ALI score when viewing fish of the opposite sex, while yellow males had a positive relationship between the two variables (Opposite: $p = 0.07$, Table S.6). All other main and interaction effects of time spent "freaking-out," number of squares entered during "the freak-out period," and the log of time to emerge were non-significant with respect to LI and ALI (Table S.6).

The total number of squares entered was negatively related to the ALI in the mirror octagon (*p* = 0.03, Table S.6), but was not significant either as a main effect or as an interaction with sex and color morph with respect to any of the other LI or ALI measures (Table S.6). The proportion of corner squares entered was not significant either as a main or interaction effect with sex and color morph with respect to any of the LI or ALI measures (Table S.6). The proportion of middle squares entered was negatively related to LI in the mirror octagon and positively related to ALI in the mirror octagon (LI: *p* = 0.03; ALI: *p* = 0.04, Table S.6) but only females and red males followed the pattern as yellow males had a positive relationship between the proportion of middle squares entered and the LI in the mirror octagon (*p* = 0.06, Table S.6). None of the other main or interaction effects with proportion of middle squares and LI or ALI were significant (Table S.6). The proportion of edge squares entered was positively related to LI in the mirror octagon and negatively related to ALI in the mirror octagon (LI: *p* = 0.02; ALI: *p* = 0.04, Table S.6), but was not significant as a main with respect to any of the other LI or ALI measures or for any of the interactions with sex and color morph (Table S.6).

Males that spent more time in corner squares were more likely to use their left eye (negative LI scores) when viewing male stimuli in the circular lateralization task while females who spent more time in corner squares were more apt to use their right eye (positive LI scores) when viewing male stimuli (*p* = 0.09, Table S.6). All other interaction effects with respect to LI and ALI were non-significant as were all the main effects of time spent in corner squares (Table S.6). Time spent in edge squares was not significant as a main effect on LI and ALI in any of the tests (Table S.6) but for females time spent in edge squares tended to be more negatively related to LI in the circular lateralization task with male stimuli while males tended to be more positively related to LI when viewing male stimuli (*p* = 0.08, Table S.6). All other interaction effects of time spent in edge squares with sex and color morph with respect to LI and ALI from other tests were non-significant (Table S.6). Time spent in middle squares was non-significant in all main and interaction effects for either LI or ALI (Table S.6).

Discussion

My analysis of the outcome measures from the boldness and lateralization tasks revealed six different relationships all of which were focused on the mirror octagon outcome measures and the outcome measures from the open field boldness task. The first relationship indicates that the time spent "freaking-out" shares a slightly positive relationship with ALI in the mirror octagon; the more time the fish spent "freaking-out" the more strongly lateralized the fish was in the mirror octagon (Figure S.30).

The second relationship I observed was that the total number of squares entered shares a moderately strong negative relationship with the ALI from the mirror octagon; the more squares entered the less strongly lateralized the fish (Figure S.31). The number of squares entered is more of an activity measure than a boldness measure and this relationship suggests that more active fish are less strongly lateralized (meaning that fish are showing less of a preference for one eye over another). This would make sense from an evolutionary standpoint as more active fish would need to be more aware of their surroundings to as to avoid getting eaten by a predator.

The third relationship I discovered was between the proportion of middle squares entered and the LI in the mirror octagon. The greater the proportion of middle squares entered the more negative the lateralization index (more left eye use, Figure S.32). This relationship indicates that bolder fish are left eye biased towards looking at their mirror image. A fourth relationship also existed between the proportion of middle squares entered, but in this case with respect to the ALI in the mirror octagon (Figure S.33). The greater the proportion of middle squares entered, the more strongly lateralized the fish were in the mirror octagon. Together these last two relationships imply that bold fish are more likely to use their left eye and be more strongly lateralized in their eye preference. It is as of yet unclear why bold fish would be preferentially biased towards their left eye when they show no preferential LI biases under any other conditions.

The fifth and sixth relationships were between the proportion of edge squares entered and the LI (Figure S.34) and between the proportion of edge squares entered and the ALI (Figure S.35). The greater the proportion of edge squares entered, the less negative (less biased) the fish's LI score was and the less strongly lateralized the fish was in the mirror octagon. These relationships imply that fish falling into the mid-range of the bold-shy spectrum are less biased (and less strongly so) in their use of one eye over another.

Principal Component Analyses

I ran a principal component analysis (PCA) , using the R function princomp(), on the outcomes of the mirror aggression task, including: time to first aggressive action and number of aggressive actions performed (bites, charges, lateral displays, and tail beats; Table S.7). The result of the PCA reveals that just under 60% of the variance is accounted for by the first component, in which time to first aggressive action was given a positive loading value while all the other aggressive outcomes had negative loading values. The loading values on component one suggest that all the aggressive behaviors shape the value of component one fairly equally and that as time to aggressive action decreases all the other measures of aggression increase. This demonstrates that principle component one is assessing overall aggression. The second component accounted for approximately 15% of the variance and treated number of bites and number of lateral displays differently from the other outcomes (giving them negative loading values rather than positive ones). Component two appears to be about the speed of escalation, since the positive loading values are assigned to the behavioral outcomes that lean towards escalating the fight more slowly rather than a quick escalation or deterring the fight from occurring. The value of component two appears to be mainly impacted by the number of lateral displays. The third component added nearly 14% to the variance accounted for and it assigned the time to first aggressive action, number of lateral displays, and number of tail beats negative loading values, while only number of bites and number of charges received positive loading values. Component three's value is heavily driven by the number of lateral displays and directionality of the loadings could indicate that this component is all about speedy escalation of the fight and attempting to resolve a fight.

A PCA was also run on the outcomes from the open field exploration task, which included the total number of squares entered, time spent in corner/middle/edge squares, and proportion of corner/middle/edge squares entered (Table S.8). The results revealed that the first two components accounted for almost 70% of the variance (component one made up 36% of the variance while component two accounted for another 33% of the variance). The first component assigned a positive loading value to the time spent in edge squares, the proportion of middle squares entered, and the total number of squares entered, while all the other measures received negative loading values; component one appears to assess the activity level of the fish. Time spent in edge squares and proportion of middle squares entered are the driving forces behind the value of component one. In the second component, time spent in middle squares, time spent in edge squares, and the proportion of edge squares entered were assigned negative loading values while all the others (time spent in corner squares, proportion of corner and middle squares entered, and the total number of squares entered) were given positive ones. The proportion of edge squares entered appears to be driving the value of component two. Component two seems to identify active but shy fish. Component three only accounted for just under an additional 13% of the variance; the total number of squares entered had the strongest loading value, suggesting that this is the driving force behind the value of component three. Proportion of edge squares entered did not factor into component three at all. Component three is about identifying the less shy fish.

The top two components from the previous PCAs were extracted and added back to the other outcome measures for a final PCA on the entire testing procedure. The outcomes extracted from the lateralization tasks that were deemed the most appropriate and meaningful measures were the ALI values. Running a full PCA on the first two components from the aggression task, the first two components from the open field exploration task, the log time to emerge in the novel environment, and the five ALI measures from the different lateralization conditions (mirror octagon, male and female stimuli, and same and opposite-sex stimuli) revealed that component one accounted for 31% of the variance and was comprised of all but two of the outcome measures (Table S.9). The excluded outcome measures were the second components extracted from the aggression and open field PCAs. All of the outcome measures had negative loading values except for the first PCA component from the open field task, which instead had a positive loading value. The value of component one is most influenced by all four ALI measures from the circular lateralization conditions (the male and female stimuli conditions share measurements with the same and opposite-sex stimuli conditions). Component one suggests that activity is the best predictor of our fish behavior. Component two accounted for an additional 13% of the variance in the data and was most heavily impacted by the time to emerge into a novel environment and the first aggression component. The second component from the open field task PCA was again excluded from this component as was the ALI from the circular lateralization task with female stimuli. The first PCA component from the open field task, the circular lateralization tasks with male, same-sex and opposite-sex stimuli were all given negative loading values The first aggression component and the time to emerge are the main impacts behind component two for the overall data. Together this suggests that aggression, boldness, and mirror octagon lateralization strength are the behaviors that best explain the data after accounting for activity level. Component three only adds about 12% to the explained variance of the data and only the ALI from the mirror octagon was given a negative loading value. The open field exploration component one, time to emerge into a novel environment, ALI from the circular lateralization task with male stimuli, and ALI from the circular lateralization task with stimuli of the same sex did not factor into the third component at all. The second open field exploration component is the driving force behind the value of component three and this component seems to explain fish that fall into a sort of middle ground on the boldness and aggression measures.

The results from the overall PCA, seem to suggest that none of these behavioral outcome measures (or PCA components) can really adequately explain the pattern of all of the data alone. There are certain combinations of behavioral outcome measures that better explain the pattern of data in a given test, but all of the variables measured, other than the second component from the open field task, have some meaningful contribution to the overall pattern of data.

Multidimensional Scaling

I used the cmdscale() function in R for MDS (Kruskal & Wish, 1978) to visually identify how closely related or dissimilar the sex and color morph groups were from one another and ran the MDS on all outcome variables (excluding a few that were derivatives of one another such as the log time to emerge). An initial plotting of the scree revealed that four dimensions would reveal the most meaningful groupings. The results show no clear indication of divisions between the sex and color morphs, while variable three shows that there are some definitive outliers in the data (Figure S.36).

Conclusion

My first two comparisons in this section looked at tasks that attempt to measure similar behaviors (boldness or lateralization) and my results suggest that there is a high degree of relatedness among the tasks and across measures. Supporting the use of these measures and providing evidence of personality in kribensis.

Looking first at the boldness comparisons, males demonstrated a high degree of relatedness between the two tasks and females showed a strong, but more tangential relationship based on all expectations. For lateralization, three of the tests were related and each displayed moderately strong relationships between their ALI measures (strength of lateralization) with one of the other tests, while the other two tests were linked to each other. These results suggested that the strength of lateralization is a persistent behavior that occurs regardless of the situation or the stimuli.

When looking at the comparison of aggression to boldness and lateralization, the results paint a fairly complex picture. It does appear that biting behaviors (time spent and number of attacks) and time to first aggressive action are strongly related to several measures of boldness including: proportion and time in edge squares, proportion of middle squares, time spent in corner squares, and log time to emerge scores. Perhaps this is suggestive of an underlying connection between the pairs of behaviors, such as bolder fish being more apt to escalate an encounter and thus perform more biting behaviors (a stronger aggressive action) and begin aggressing earlier. It also appears that time to emerge into the open field environment shares some underlying mechanism with the latency to first aggressive action as both are generally positively related to one another.

When looking at the results based on sex and color morph one thing that is readily apparent is that aggressive and non-aggressive females are quite different with respect to boldness and lateralization (non-aggressive females are less bold and more left eye biased) while males of either morph type seem to be rather similar regardless of the aggressive and non-aggressive distinctions. In comparing how all females compare to the male morph types no clear pattern emerges. Females followed the red morph pattern of behavior with respect to time spent in corner squares (Figure S.18) and time spent in edge squares (Figure S.22). Alternatively, females were more similar to the pattern of behavior of yellow males with regards to lateralization in the mirror octagon (Figure S.29) and were not at all related to either male morph type with regards to the proportion of edge squares entered (Figure S.12), proportion of middle squares entered (Figure S.16), and log emerge time (Figure S.26).

Since females have been identified as having red and yellow males (Axelrod, 1993) and females that developed at a lower pH display higher aggression than females at higher pHs (Reddon & Hurd, 2013) it is possible that the classification of aggressive or not aggressive is actually identifying female color morphs. If this is the case then we would expect that females produced at lower pHs would be most closely related in behavior to red males since they are more commonly produced at lower pHs. This is hardly supported by the cases where aggressive and non-aggressive females were significantly different from one another.

Conversely, if we were to simply compare males classified as aggressive or non-aggressive we would instead see that males are generally similar regardless of aggressive classification. So if these differences between aggressive and non-aggressive females is not related to morph classification, then what other explanations are available? Perhaps instead what we are seeing is instead related to the breeding readiness of the females, however, a caveat of this proposal is that it is likely the females breeding readiness varied over the course of the experiment.

Finally, for the measures of boldness, in particular; the time spent “freaking-out”, total number of squares visited, and proportions of middle and edge squares entered, are strongly related to lateralization measures from the mirror octagon task. From the results it seems that strongly lateralized fish had longer “freak-out” times, lower overall activity in the open field task, and entered a larger portion of middle squares, but entered a smaller proportion of edge squares. Fish that entered a greater proportion of middle squares were more left eye lateralized (negative scores), while fish that entered more edge squares were more right eye lateralized (positive scores).

The results of the PCAs and their components suggest that most of the scoring measures and tests used in the experiment add some clarity to the data as no one measure or test is able to explain the pattern of the data as a whole. The results of the MDS indicate that the resultant data from the experiment is a complicated collection of information and that there are several fish that seem to fall outside of the range of normal.

What is abundantly clear from the comparative relationships between the aggression and boldness tasks and the boldness and lateralization tasks is that there must be at least two underpinning relationships between the personality measures in my study. The mirror aggression and the boldness tasks do suggest that aggression and boldness are strongly related with a general trend of if a fish is aggressive it will also be bolder than a non-aggressive fish. This relationship also reveals patterns of behavior between the different sexes and color morphs that is not readily apparent from the one-way ANOVAs. The open field task and the mirror octagon are also strongly related. It is also clear that population level lateralization is present but it is not based on populations of sex or color morph, but is instead based on the shy-bold behavioral axis.

References

Adams, C.F., Liley, N.R., & Gorzalka, B. B. (1996). PCPA increases aggression in male firemouth cichlids. *Pharmacology,* 53(5), 328-330. doi: 10.1159/000139446

Axelrod, H. R. (1996). *The most complete colored lexicon of cichlids* (2nd ed.). Neptune City, T.F.H. Publications, Inc.

Bisazza, A., Facchin, L., Pignatti, R., & Vallortigara, G. (1998). Lateralization of detour behaviour in poeciliid fish: the effect of species, gender and sexual motivation. *Behavioural Brain Research*, *91*(1-2), 157–64. doi: 10.1016/S0166-4328(97)00114-9

Brown, C., & Braithwaite, V. A. (2004). Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. *Animal Behaviour*, *68*(6), 1325–1329. doi:10.1016/j.anbehav.2004.04.004

Brown, C., Burgess, F., & Braithwaite, V. A. (2007). Heritable and experiential effects on boldness in a tropical poeciliid. *Behavioral Ecology and Sociobiology*, *62*(2), 237–243. doi:10.1007/s00265-007-0458-3

Brown, C., Gardner, C., & Braithwaite, V. A. (2004). Population variation in lateralized eye use in the poeciliid Brachyraphis episcopi. *Proceedings. Biological Sciences / The Royal Society*, *271 Suppl* , S455–7. doi:10.1098/rsbl.2004.0222

Brown, C., & Irving, E. (2014). Individual personality traits influence group exploration in a feral guppy population. *Behavioral Ecology*, *25*(1), 95–101. doi:10.1093/beheco/art090

Brown, C., Jones, F., & Braithwaite, V. (2005). In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, *70*(5), 1003–1009. doi:10.1016/j.anbehav.2004.12.022

Burns, J. G. (2008). The validity of three tests of temperament in guppies (Poecilia reticulata). *Journal of Comparative Psychology (Washington, D.C. : 1983)*, *122*(4), 344–56. doi:10.1037/0735-7036.122.4.344

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, *88*, 465–475. doi:10.1111/brv.12007

Chang, C., Li, C.-Y., Earley, R. L., & Hsu, Y. (2012). Aggression and related behavioral traits: the impact of winning and losing and the role of hormones. *Integrative and Comparative Biology*, *52*(6), 801–13. doi:10.1093/icb/ics057

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *The Journal of Animal Ecology*, *76*(6), 1128–38. doi:10.1111/j.1365-2656.2007.01284.x

Facchin, L., Bisazza, A., & Vallortigara, G. (1999). What causes lateralization of detour behavior in fish? Evidence for asymmetries in eye use. *Behavioural Brain Research*, *103*(2), 229–34. doi:10.1016/S0166-4328(99)00043-1

Franck, D., & Ribowski, A. (1987). Influences of prior agonistic experiences on aggression measures in the male swordtail (*Xiphophorus helleri*). *Behaviour*, *103*(1), 217–240. doi:10.1163/156853987X00369

Hsu, Y., Earley, R. L., & Wolf, L. L. (2006). Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biological Reviews of the Cambridge Philosophical Society*, *81*(1), 33–74. doi:10.1017/S146479310500686X

Kruskal, J.B. & Wish, M. (1978). *Multidimensional scaling*. E. M. Uslander (Ed.). Quantitative Applications in the Social Sciences. Beverly Hills, CA: Sage Publications LTD.

Moscicki, M. K., & Hurd, P.L. (2014). *Sex, prior, and current stress exposure affect exploration and behavioural syndromes in convict cichlids (Amatitlania nigrofasciata)*. Manuscript in preparation.

Northmore, D. (2011). *Optic Tectum*. *Encyclopedia of Fish Physiology: From Genome to Environment* (Vol. 1, pp. 131–142). Elsevier Inc. doi:10.1016/B978-0-12-374553-8.00093-9

Reddon, A. R., & Hurd, P. L. (2008). Aggression, sex and individual differences in cerebral lateralization in a cichlid fish. *Biology Letters*, *4*(4), 338–40. doi:10.1098/rsbl.2008.0206

Reddon, A. R., & Hurd, P. L. (2009). Individual differences in cerebral lateralization are associated with shy–bold variation in the convict cichlid. *Animal Behaviour*, *77*(1), 189–193. doi:10.1016/j.anbehav.2008.09.026

Reddon, A. R., & Hurd, P. L. (2013). Water pH during early development influences sex ratio and male morph in a West African cichlid fish, Pelvicachromis pulcher. *Zoology (Jena, Germany)*, 1–5. doi:10.1016/j.zool.2012.11.001

Snekser, J. L., & Itzkowitz, M. (2014). Contrasting Parental Tasks Influence Parental Roles for Paired and Single Biparental Cichlid Fish. *Ethology*, *120*(5), 483–491. doi:10.1111/eth.12221

Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A Methodological Review of Personality-Related Studies in Fish: Focus on the Shy-Bold Axis of Behavior. *International Journal of Comparative Psychology*, *23*(1), 1–25.

Table S.1 ANOVA output of fish condition, standard length and mass at the time of testing and sex/color morph. Pairwise *t*-tests reveal the differences between groups with respect to either fish condition, standard length, or mass.

	Condition	**Standard Length**	**Mass**
Mirror Aggression	F(2, 134) = 1.58, $p = 0.21$	F(2, 134) = 38.62 $p < 0.001$	F(2, 134) = 20.51 $p < 0.001$
Females vs. Yellow males	$p = 0.99$	$p < 0.001$	$p < 0.001$
Females vs. Red males	$p = 0.10$	$p < 0.001$	$p = 0.16$
Yellow males vs. Red Morph	$p = 0.09$	$p = 0.04$	$p = 0.009$
Open Field	F(2, 133) =4.09, $p = 0.02$	F(2, 133) = 51.48, $p < 0.001$	F(2, 133) = 29.64, $p < 0.001$
Females vs. Yellow males	$p = 0.79$	$p < 0.001$	$p < 0.001$
Females vs. Red males	$p = 0.01$	$p < 0.001$	$p = 0.16$
Yellow males vs. Red Morph	$p = 0.01$	$p = 0.04$	$p = 0.001$
Novel Environment	F(2, 130) = 0.67, $p = 0.52$	F(2, 130) = 52.14, $p < 0.001$	F(2, 130) = 26.71 $p < 0.001$
Females vs. Yellow males	$p = 0.55$	$p < 0.001$	$p < 0.001$
Females vs. Red males	$p = 0.26$	$p = 0.001$	$p = 0.06$
Yellow males vs. Red Morph	$p = 0.43$	$p = 0.002$	$p = 0.005$
Mirror Octagon	F(2, 134) = 1.69, $p = 0.19$	F(2, 134) = 61.86, $p < 0.001$	F(2, 134) = 34.84, $p < 0.001$
Females vs. Yellow males	$p = 0.96$	$p < 0.001$	$p < 0.001$
Females vs. Red males	$p = 0.09$	$p < 0.001$	$p = 0.004$
Yellow males vs. Red Morph	$p = 0.08$	$p = 0.09$	$p = 0.02$
Circular Lateralization with Male Stimuli	F(2, 132) = 28.98, $p < 0.001$	F(2, 132) = 1.84, $p < 0.001$	F(2, 132) = 30.87, $p < 0.001$
Females vs. Yellow males	$p < 0.01$	$p < 0.001$	$p < 0.001$
Females vs. Red males	$p < 0.001$	$p < 0.001$	$p = 0.009$
Yellow males vs. Red Morph	$p = 0.04$	$p < 0.07$	$p = 0.02$
Circular Lateralization with Female Stimuli	F(2, 131) = 0.64, $p = 0.53$	F(2, 131) = 94.67, $p < 0.001$	F(2, 131) = 42.76, $p < 0.001$
Females vs. Yellow males	$p = 0.32$	$p < 0.001$	$p < 0.001$
Females vs. Red males	$p = 0.90$	$p < 0.001$	$p < 0.001$
Yellow males vs. Red Morph	$p = 0.44$	$p = 0.001$	$p = 0.06$
Circular Lateralization with Same-sex Stimuli	F(2, 132) = 34.72, $p < 0.01$	F(2, 132) = 1.91, $p < 0.001$	F(2, 132) = 37.06, $p < 0.001$
Females vs. Yellow males	$p = 0.06$	$p < 0.001$	$p < 0.001$
Females vs. Red males	$p = 0.002$	$p < 0.001$	$p = 0.003$
Yellow males vs. Red Morph	$p < 0.05$	$p = 0.06$	$p = 0.01$
Circular Lateralization with Opposite-sex Stimuli	F(2, 131) = 1.29, $p = 0.28$	F(2, 131) = 84.14, $p < 0.001$	F(2, 131) = 35.54, $p < 0.001$
Females vs. Yellow males	$p = 0.13$	$p < 0.001$	$p < 0.001$
Females vs. Red males	$p = 0.89$	$p < 0.001$	$p = 0.001$
Yellow males vs. Red Morph	$p = 0.40$	$p = 0.002$	$p = 0.07$

Table S.2 Relationships between boldness measures (open field behavior outcomes and novel environment behavior outcomes).

	Main effect	**Sex/Color Morph**	**Interaction**
Total squares entered on log of time to emerge	F(2,130) = 0.44, $p = 0.51$	F(2, 130) = 1.43, $p = 0.24$	F(2, 130) = 2.65, $p = 0.07$
Proportion of corner squares entered on log of time to emerge	F(2, 130) = 1.11, $p = 0.29$	F(2, 130) = 3.24, $p = 0.04$	F(2, 130) = 0.82, $p = 0.44$
Proportion of middle squares entered on log of time to emerge	F(2, 130) = 2.06, $p = 0.15$	F(2, 130) = 2.32, $p = 0.10$	F(2, 130) = 1.52, $p = 0.22$
Proportion of edge squares entered on log of time to emerge	F(2, 130) = 0.60, $p = 0.44$	F(2, 130) = 1.81, $p = 0.17$	F(2, 130) = 1.19, $p = 0.31$
Time spent in corner squares entered on log of time to emerge	F(2, 130) = 0.02, $p = 0.90$	F(2, 130) = 2.18, $p = 0.12$	F(2, 130) = 0.80, $p = 0.45$
Time spent in edge squares entered on log of time to emerge	F(2, 130) = 0.002, $p = 0.97$	F(2, 130) = 1.92, $p = 0.15$	F(2, 130) = 0.30, $p = 0.74$
Time spent in middle squares entered on log of time to emerge	F(2, 130) = 3.12, $p = 0.08$	F(2, 130) = 1.46, $p = 0.24$	F(2, 130) = 13.14, $p < 0.001$
Time spent “freaking-out” on log of time to emerge	F(2, 130) = 2.51, $p = 0.12$	F(2, 130) = 1.85, $p = 0.16$	F(2, 130) = 0.27, $p = 0.76$
Number of squares entered during “the freak-out period” on log of time to emerge	F(2, 130) = 3.44, $p = 0.07$	F(2, 130) = 1.76, $p = 0.18$	F(2, 130) = 0.45, $p = 0.64$

Table S.3. Relationships between lateralization measures.

	Main Effect	**Sex/Color Morph**	**Interaction**
Mirror Octagon LI			
vs. circular lateralization with male stimuli	F(2, 132) = 1.02, *p* = 0.31	F(2, 132) = 0.42, *p* = 0.66	F(2, 132) = 0.56, *p* = 0.57
vs. circular lateralization with female stimuli	F(2, 131) = 0.28, *p* = 0.60	F(2, 131) = 0.41, *p* = 0.66	F(2, 131) = 1.62, *p* = 0.20
vs. circular lateralization with same-sex stimuli	F(2, 132) = 0.22, *p* = 0.64	F(2, 132) = 0.19, *p* = 0.82	F(2, 132) = 0.24, *p* = 0.79
vs. circular lateralization with opposite-sex stimuli	F(2, 131) = 1.24, *p* = 0.27	F(2, 131) =0.02, *p* = 0.98	F(2, 131) = 2.26, *p* = 0.11
Mirror Octagon ALI			
vs. circular lateralization with male stimuli	F(2, 132) = 0.49, *p* = 0.49	F(2, 132) = 1.48, *p* = 0.23	F(2, 132) = 0.01, *p* = 0.99
vs. circular lateralization with female stimuli	F(2, 131) = 4.24, *p* = 0.04	F(2, 131) = 1.10, *p* = 0.34	F(2, 131) = 0.05, *p* = 0.95
vs. circular lateralization with same-sex stimuli	F(2, 132) = 3.81, *p* = 0.053	F(2, 132) = 3.24, *p* = 0.04	F(2, 132) = 0.33, *p* = 0.72
vs. circular lateralization with opposite-sex stimuli	F(2, 131) = 0.53, *p* = 0.47	F(2, 131) = 1.21, *p* = 0.30	F(2, 131) = 0.18, *p* = 0.84
Circular lateralization LI			
Male stimuli vs. Female stimuli	F(2, 131) = 0.22, *p* = 0.64	F(2, 131) = 0.49, *p* = 0.61	F(2, 131) = 0.33, *p* = 0.72
Same-sex vs. Opposite-sex stimuli	F(2, 131) = 0.28, *p* = 0.60	F(2, 131) = 0.05, *p* = 0.95	F(2, 131) = 0.29, *p* = 0.75
Circular lateralization ALI			
Male stimuli vs. Female stimuli	F(2, 131) = 5.38, *p* = 0.02	F(2, 131) = 0.13, *p* = 0.88	F(2, 131) = 1.84, *p* = 0.16
Same-sex vs. Opposite-sex stimuli	F(2, 131) = 6.38, *p* = 0.01	F(2, 131) = 1.15, *p* = 0.32	F(2, 131) = 1.03, *p* = 0.36

Table S.4. Relationships between aggression and boldness measures.

	Main Effect	**Sex/Color Morph**	**Interaction**
Time to first aggressive action vs.			
Time spent “freaking-out”	F(2, 133) = 0.34, p = 0.56	F(2, 133) = 1.64, p = 0.20	F(2, 133) = 1.85, p = 0.16
Number of squares entered during “the freak-out period”	F(2, 133) = 1.13, p = 0.29	F(2, 133) = 1.15, p = 0.32	F(2, 133) = 1.65, p = 0.20
Total number of squares entered	F(2, 133) = 0.00, p = 0.99	F(2, 133) = 1.90, p = 0.15	F(2, 133) = 1.00, p = 0.37
Proportion of corner squares entered	F(2, 133) = 0.80, p = 0.37	F(2, 133) = 0.23, p = 0.79	F(2, 133) = 0.30, p = 0.74
Proportion of middle squares entered	F(2, 133) = 4.48, p = 0.04	F(2, 133) = 1.94, p = 0.15	F(2, 133) = 1.95, p = 0.15
Proportion of edge squares entered	F(2, 133) = 7.83, p = 0.006	F(2, 133) = 3.09, p = 0.05	F(2, 133) = 3.16, p = 0.046
Time spent in corner squares	F(2, 133) = 8.64, p = 0.004	F(2, 133) = 1.09, p = 0.34	F(2, 133) = 2.29, p = 0.11
Time spent in edge squares	F(2, 133) = 9.57, p = 0.002	F(2, 133) = 4.49, p = 0.01	F(2, 133) = 5.34, p = 0.01
Time spent in middle squares	F(2, 133) = 0.08, p = 0.78	F(2, 133) = 3.68, p = 0.03	F(2, 133) = 1.66, p = 0.19
Log time to emerge	F(2, 133) = 6.43, p = 0.01	F(2, 133) = 0.27, p = 0.77	F(2, 133) = 2.68, p = 0.07
Aggressive or Non-Aggressive vs.			
Time spent “freaking-out”	F(2, 133) = 0.27, *p* = 0.61	F(2, 133) = 0.93, *p* = 0.40	F(2, 133) = 1.73, *p* = 0.18
Number of squares entered during “the freak-out period”	F(2, 133) = 1.39, *p* = 0.24	F(2, 133) = 1.19, *p* = 0.31	F(2, 133) = 1.48, *p* = 0.23
Total number of squares entered	F(2, 133) = 1.33, *p* = 0.25	F(2, 133) = 3.10, *p* = 0.048	F(2, 133) = 1.52, *p* = 0.22
Proportion of corner squares entered	F(2, 133) = 1.60, *p* = 0.21	F(2, 133) = 0.25, *p* = 0.78	F(2, 133) = 0.52, *p* = 0.60
Proportion of middle squares entered	F(2, 133) = 7.74, *p* = 0.006	F(2, 133) = 2.47, *p* = 0.09	F(2, 133) = 3.76, *p* = 0.03
Proportion of edge squares entered	F(2, 133) = 14.24, *p* < 0.001	F(2, 133) = 2.90, *p* = 0.06	F(2, 133) = 6.04, *p* = 0.003
Time spent in corner squares	F(2, 133) = 15.95, *p* < 0.001	F(2, 133) = 4.01, *p* = 0.02	F(2, 133) = 4.90, *p* = 0.009
Time spent in edge squares	F(2, 133) = 19.68, *p* < 0.001	F(2, 133) = 4.85, *p* = 0.009	F(2, 133) = 9.71, *p* < 0.001
Time spent in middle squares	F(2, 133) = 0.07, *p* = 0.79	F(2, 133) = 0.06, *p* = 0.94	F(2, 133) = 1.39, *p* = 0.25
Log time to emerge	F(2, 133) = 4.67, *p* = 0.03	F(2, 133) = 9.96, *p* < 0.001	F(2, 133) = 4.29, *p* = 0.02

Table S.4. (continued)

	Main Effect	**Sex/Color Morph**	**Interaction**
Number of bites vs.			
Time spent "freaking-out"	F(2, 133) 0.21, $p = 0.65$	F(2, 133) 0.34, $p = 0.71$	F(2, 133) 1.09, $p = 0.34$
Number of squares entered during "the freak-out period"	F(2, 133) 0.04, $p = 0.83$	F(2, 133) 0.80, $p = 0.45$	F(2, 133) 1.12, $p = 0.33$
Total number of squares entered	F(2, 133) 0.04, $p = 0.85$	F(2, 133) 1.06, $p = 0.35$	F(2, 133) 0.98, $p = 0.38$
Proportion of corner squares entered	F(2, 133) 1.33, $p = 0.25$	F(2, 133) 0.07, $p = 0.93$	F(2, 133) 0.16, $p = 0.85$
Proportion of middle squares entered	F(2, 133) 4.63, $p = 0.03$	F(2, 133) 0.64, $p = 0.53$	F(2, 133) 1.32, $p = 0.27$
Proportion of edge squares entered	F(2, 133) 9.22, $p = 0.003$	F(2, 133) 0.70, $p = 0.50$	F(2, 133) 2.12, $p = 0.12$
Time spent in corner squares	F(2, 133) 16.88, $p < 0.001$	F(2, 133) 4.36, $p = 0.01$	F(2, 133) 5.52, $p = 0.01$
Time spent in edge squares	F(2, 133) 16.23, $p < 0.001$	F(2, 133) 3.16, $p = 0.05$	F(2, 133) 7.71, $p < 0.001$
Time spent in middle squares	F(2, 133) 0.01, $p = 0.93$	F(2, 133) 1.01, $p = 0.37$	F(2, 133) 0.16, $p = 0.85$
Log time to emerge	F(2, 133) 3.99, $p = 0.048$	F(2, 133) 3.32, $p = 0.04$	F(2, 133) 0.46, $p = 0.63$
Number of charges vs.			
Time spent "freaking-out"	F(2, 133) 0.21, $p = 0.65$	F(2, 133) 0.11, $p = 0.89$	F(2, 133) 0.35, $p = 0.71$
Number of squares entered during "the freak-out period"	F(2, 133) 0.00, $p = 1.00$	F(2, 133) 0.22, $p = 0.80$	F(2, 133) 0.15, $p = 0.86$
Total number of squares entered	F(2, 133) 0.41, $p = 0.52$	F(2, 133) 1.58, $p = 0.21$	F(2, 133) 5.39, $p = 0.006$
Proportion of corner squares entered	F(2, 133) 0.16, $p = 0.69$	F(2, 133) 0.17, $p = 0.84$	F(2, 133) 0.16, $p = 0.85$
Proportion of middle squares entered	F(2, 133) 2.54, $p = 0.11$	F(2, 133) 0.24, $p = 0.79$	F(2, 133) 0.68, $p = 0.51$
Proportion of edge squares entered	F(2, 133) 1.75, $p = 0.19$	F(2, 133) 0.04, $p = 0.96$	F(2, 133) 0.46, $p = 0.63$
Time spent in corner squares	F(2, 133) 3.67, $p = 0.06$	F(2, 133) 1.05, $p = 0.35$	F(2, 133) 0.95, $p = 0.39$
Time spent in edge squares	F(2, 133) 2.48, $p = 0.12$	F(2, 133) 0.54, $p = 0.58$	F(2, 133) 1.77, $p = 0.17$
Time spent in middle squares	F(2, 133) 0.00, $p = 0.96$	F(2, 133) 0.94, $p = 0.39$	F(2, 133) 0.46, $p = 0.63$
Log time to emerge	F(2, 133) 1.89, $p = 0.17$	F(2, 133) 3.60, $p = 0.03$	F(2, 133) 0.28, $p = 0.76$

Table S.4. (continued)

	Main Effect	**Sex/Color Morph**	**Interaction**
Number of lateral displays vs.			
Time spent "freaking-out"	F(2, 133) 2.79, *p* = 0.10	F(2, 133) 0.76, *p* = 0.47	F(2, 133) 3.17, *p* = 0.045
Number of squares entered during "the freak-out period"	F(2, 133) 0.46, *p* = 0.50	F(2, 133) 0.71, *p* = 0.49	F(2, 133) 1.05, *p* = 0.35
Total number of squares entered	F(2, 133) 0.06, *p* = 0.81	F(2, 133) 1.34, *p* = 0.27	F(2, 133) 2.44, *p* = 0.09
Proportion of corner squares entered	F(2, 133) 0.00, *p* = 0.96	F(2, 133) 0.13, *p* = 0.88	F(2, 133) 0.06, *p* = 0.94
Proportion of middle squares entered	F(2, 133) 3.08, *p* = 0.08	F(2, 133) 0.29, *p* = 0.75	F(2, 133) 0.97, *p* = 0.38
Proportion of edge squares entered	F(2, 133) 2.98, *p* = 0.09	F(2, 133) 0.10, *p* = 0.90	F(2, 133) 1.05, *p* = 0.35
Time spent in corner squares	F(2, 133) 3.53, *p* = 0.06	F(2, 133) 1.31, *p* = 0.27	F(2, 133) 1.07, *p* = 0.34
Time spent in edge squares	F(2, 133) 2.76, *p* = 0.10	F(2, 133) 0.33, *p* = 0.72	F(2, 133) 1.54, *p* = 0.22
Time spent in middle squares	F(2, 133) 0.02, *p* = 0.89	F(2, 133) 1.31, *p* = 0.27	F(2, 133) 0.36, *p* = 0.70
Log time to emerge	F(2, 133) 2.25, *p* = 0.14	F(2, 133) 5.64, *p* = 0.005	F(2, 133) 1.01, *p* = 0.37
Number of tail beats vs.			
Time spent "freaking-out"	F(2, 133) 0.65, *p* = 0.42	F(2, 133) 0.06, *p* = 0.94	F(2, 133) 0.41, *p* = 0.67
Number of squares entered during "the freak-out period"	F(2, 133) 0.75, *p* = 0.39	F(2, 133) 0.21, *p* = 0.81	F(2, 133) 0.25, *p* = 0.78
Total number of squares entered	F(2, 133) 0.00, *p* = 0.95	F(2, 133) 1.82, *p* = 0.17	F(2, 133) 1.82, *p* = 0.17
Proportion of corner squares entered	F(2, 133) 0.01, *p* = 0.93	F(2, 133) 0.12, *p* = 0.89	F(2, 133) 0.10, *p* = 0.91
Proportion of middle squares entered	F(2, 133) 0.00, *p* = 0.96	F(2, 133) 0.11, *p* = 0.89	F(2, 133) 0.39, *p* = 0.68
Proportion of edge squares entered	F(2, 133) 0.00, *p* = 0.99	F(2, 133) 0.02, *p* = 0.98	F(2, 133) 0.61, *p* = 0.55
Time spent in corner squares	F(2, 133) 1.18, *p* = 0.28	F(2, 133) 0.44, *p* = 0.64	F(2, 133) 0.13, *p* = 0.88
Time spent in edge squares	F(2, 133) 0.94, *p* = 0.33	F(2, 133) 0.15, *p* = 0.86	F(2, 133) 0.47, *p* = 0.62
Time spent in middle squares	F(2, 133) 0.09, *p* = 0.76	F(2, 133) 1.26, *p* = 0.29	F(2, 133) 0.67, *p* = 0.51
Log time to emerge	F(2, 133) 0.50, *p* = 0.48	F(2, 133) 4.58, *p* = 0.01	F(2, 133) 1.14, *p* = 0.32

Table S.4. (continued)

	Main Effect	**Sex/Color Morph**	**Interaction**
Duration of bites vs.			
Time spent “freaking-out”	F(2, 133) 0.00, $p = 0.96$	F(2, 133) 0.22, $p = 0.80$	F(2, 133) 0.89, $p = 0.41$
Number of squares entered during “the freak-out period”	F(2, 133) 0.26, $p = 0.61$	F(2, 133) 0.73, $p = 0.48$	F(2, 133) 1.09, $p = 0.34$
Total number of squares entered	F(2, 133) 0.06, $p = 0.81$	F(2, 133) 0.78, $p = 0.46$	F(2, 133) 0.57, $p = 0.57$
Proportion of corner squares entered	F(2, 133) 1.04, $p = 0.31$	F(2, 133) 0.09, $p = 0.91$	F(2, 133) 0.20, $p = 0.82$
Proportion of middle squares entered	F(2, 133) 3.68, $p = 0.06$	F(2, 133) 0.55, $p = 0.58$	F(2, 133) 1.25, $p = 0.29$
Proportion of edge squares entered	F(2, 133) 7.24, $p = 0.01$	F(2, 133) 0.59, $p = 0.56$	F(2, 133) 2.13, $p = 0.12$
Time spent in corner squares	F(2, 133) 14.53, $p < 0.001$	F(2, 133) 4.04, $p = 0.02$	F(2, 133) 5.59, $p = 0.005$
Time spent in edge squares	F(2, 133) 13.07, $p < 0.001$	F(2, 133) 2.94, $p = 0.06$	F(2, 133) 7.86, $p < 0.001$
Time spent in middle squares	F(2, 133) 0.02, $p = 0.88$	F(2, 133) 1.02, $p = 0.36$	F(2, 133) 0.11, $p = 0.89$
Log time to emerge	F(2, 133) 8.71, $p = 0.004$	F(2, 133) 4.93, $p = 0.01$	F(2, 133) 1.84, $p = 0.16$
Duration of charges vs.			
Time spent “freaking-out”	F(2, 133) 0.37, $p = 0.54$	F(2, 133) 0.17, $p = 0.84$	F(2, 133) 0.55, $p = 0.58$
Number of squares entered during “the freak-out period”	F(2, 133) 0.06, $p = 0.81$	F(2, 133) 0.32, $p = 0.73$	F(2, 133) 0.29, $p = 0.75$
Total number of squares entered	F(2, 133) 0.30, $p = 0.59$	F(2, 133) 1.82, $p = 0.17$	F(2, 133) 4.48, $p = 0.01$
Proportion of corner squares entered	F(2, 133) 0.89, $p = 0.35$	F(2, 133) 0.18, $p = 0.83$	F(2, 133) 0.20, $p = 0.82$
Proportion of middle squares entered	F(2, 133) 1.81, $p = 0.18$	F(2, 133) 0.17, $p = 0.85$	F(2, 133) 0.36, $p = 0.70$
Proportion of edge squares entered	F(2, 133) 0.47, $p = 0.49$	F(2, 133) 0.02, $p = 0.98$	F(2, 133) 0.39, $p = 0.68$
Time spent in corner squares	F(2, 133) 1.10, $p = 0.30$	F(2, 133) 0.80, $p = 0.45$	F(2, 133) 0.30, $p = 0.74$
Time spent in edge squares	F(2, 133) 0.32, $p = 0.57$	F(2, 133) 0.38, $p = 0.68$	F(2, 133) 0.81, $p = 0.45$
Time spent in middle squares	F(2, 133) 0.00, $p = 0.99$	F(2, 133) 1.25, $p = 0.29$	F(2, 133) 0.18, $p = 0.83$
Log time to emerge	F(2, 133) 3.47, $p = 0.06$	F(2, 133) 5.57, $p = 0.005$	F(2, 133) 1.32, $p = 0.27$

Table S.4. (continued)

	Main Effect	**Sex/Color Morph**	**Interaction**
Duration of lateral displays vs.			
Time spent “freaking-out”	F(2, 133) 0.74, *p* = 0.39	F(2, 133) 0.04, *p* = 0.96	F(2, 133) 0.09, *p* = 0.92
Number of squares entered during “the freak-out period”	F(2, 133) 0.73, *p* = 0.39	F(2, 133) 0.13, *p* = 0.88	F(2, 133) 0.06, *p* = 0.94
Total number of squares entered	F(2, 133) 0.93, *p* = 0.34	F(2, 133) 2.56, *p* = 0.08	F(2, 133) 3.00, *p* = 0.053
Proportion of corner squares entered	F(2, 133) 0.43, *p* = 0.52	F(2, 133) 0.08, *p* = 0.92	F(2, 133) 0.07, *p* = 0.93
Proportion of middle squares entered	F(2, 133) 0.71, *p* = 0.40	F(2, 133) 0.18, *p* = 0.84	F(2, 133) 0.60, *p* = 0.55
Proportion of edge squares entered	F(2, 133) 0.15, *p* = 0.70	F(2, 133) 0.06, *p* = 0.94	F(2, 133) 0.48, *p* = 0.62
Time spent in corner squares	F(2, 133) 0.02, *p* = 0.88	F(2, 133) 0.60, *p* = 0.55	F(2, 133) 0.02, *p* = 0.98
Time spent in edge squares	F(2, 133) 0.05, *p* = 0.82	F(2, 133) 0.22, *p* = 0.80	F(2, 133) 0.60, *p* = 0.55
Time spent in middle squares	F(2, 133) 0.03, *p* = 0.86	F(2, 133) 1.67, *p* = 0.19	F(2, 133) 2.14, *p* = 0.12
Log time to emerge	F(2, 133) 0.19, *p* = 0.67	F(2, 133) 3.52, *p* = 0.03	F(2, 133) 2.10, *p* = 0.13
Duration of tail beats vs.			
Time spent “freaking-out”	F(2, 133) 0.85, *p* = 0.36	F(2, 133) 0.02, *p* = 0.98	F(2, 133) 0.17, *p* = 0.84
Number of squares entered during “the freak-out period”	F(2, 133) 0.92, *p* = 0.34	F(2, 133) 0.06, *p* = 0.94	F(2, 133) 0.18, *p* = 0.83
Total number of squares entered	F(2, 133) 0.00, *p* = 1.00	F(2, 133) 2.49, *p* = 0.09	F(2, 133) 2.57, *p* = 0.08
Proportion of corner squares entered	F(2, 133) 0.03, *p* = 0.87	F(2, 133) 0.11, *p* = 0.89	F(2, 133) 0.11, *p* = 0.89
Proportion of middle squares entered	F(2, 133) 0.02, *p* = 0.90	F(2, 133) 0.20, *p* = 0.82	F(2, 133) 0.40, *p* = 0.67
Proportion of edge squares entered	F(2, 133) 0.00, *p* = 1.00	F(2, 133) 0.06, *p* = 0.94	F(2, 133) 0.50, *p* = 0.61
Time spent in corner squares	F(2, 133) 1.14, *p* = 0.29	F(2, 133) 0.63, *p* = 0.53	F(2, 133) 0.28, *p* = 0.76
Time spent in edge squares	F(2, 133) 0.85, *p* = 0.36	F(2, 133) 0.22, *p* = 0.80	F(2, 133) 0.43, *p* = 0.65
Time spent in middle squares	F(2, 133) 0.11, *p* = 0.74	F(2, 133) 2.40, *p* = 0.09	F(2, 133) 0.04, *p* = 0.96
Log time to emerge	F(2, 133) 0.37, *p* = 0.54	F(2, 133) 5.02, *p* = 0.01	F(2, 133) 1.52, *p* = 0.22

Table S.5. Relationships between aggression and LI and ALI measures.

	Main Effect	**Sex/Color Morph**	**Interaction**
Time to first aggressive action vs.			
LI in the mirror octagon	F(2, 134) = 2.86, $p = 0.09$	F(2, 134) = 0.14, $p = 0.87$	F(2, 134) = 0.48, $p = 0.62$
ALI in the mirror octagon	F(2, 134) = 1.08, $p = 0.30$	F(2, 134) = 1.10, $p = 0.34$	F(2, 134) = 0.16, $p = 0.85$
LI with male stimuli	F(2, 132) = 0.43, $p = 0.51$	F(2, 132) = 0.14, $p = 0.87$	F(2, 132) = 0.23, $p = 0.79$
ALI with male stimuli	F(2, 132) = 0.01, $p = 0.92$	F(2, 132) = 3.78, $p = 0.03$	F(2, 132) = 0.99, $p = 0.37$
LI with female stimuli	F(2, 131) = 0.03, $p = 0.86$	F(2, 131) = 0.19, $p = 0.83$	F(2, 131) = 0.33, $p = 0.72$
ALI with female stimuli	F(2, 131) = 0.65, $p = 0.42$	F(2, 131) = 1.45, $p = 0.24$	F(2, 131) = 0.80, $p = 0.45$
LI with same-sex stimuli	F(2, 132) = 0.02, $p = 0.87$	F(2, 132) = 0.07, $p = 0.93$	F(2, 132) = 0.33, $p = 0.72$
ALI with same-sex stimuli	F(2, 132) = 0.60, $p = 0.44$	F(2, 132) = 5.85, $p = 0.004$	F(2, 132) = 1.64, $p = 0.20$
LI with opposite-sex stimuli	F(2, 131) = 0.51, $p = 0.48$	F(2, 131) = 0.28, $p = 0.76$	F(2, 131) = 0.52, $p = 0.60$
ALI with opposite-sex stimuli	F(2, 131) = 0.01, $p = 0.91$	F(2, 131) = 0.45, $p = 0.64$	F(2, 131) = 0.19, $p = 0.83$
Aggressive or Non-Aggressive vs.			
LI in the mirror octagon	F(2, 134) = 6.14, $p = 0.01$	F(2, 134) = 1.49, $p =0.23$	F(2, 134) = 1.17, $p =0.31$
ALI in the mirror octagon	F(2, 134) = 0.79, $p = 0.37$	F(2, 134) = 1.93, $p = 0.15$	F(2, 134) = 0.06, $p = 0.95$
LI with male stimuli	F(2, 132) = 0.10, $p = 0.75$	F(2, 132) = 0.98, $p = 0.38$	F(2, 132) = 0.54, $p = 0.58$
ALI with male stimuli	F(2, 132) = 0.10, $p = 0.75$	F(2, 132) = 0.31, $p = 0.73$	F(2, 132) = 0.35, $p = 0.71$
LI with female stimuli	F(2, 131) = 0.06, $p = 0.80$	F(2, 131) = 0.66, $p = 0.52$	F(2, 131) = 0.33, $p = 0.72$
ALI with female stimuli	F(2, 131) = 0.43, $p = 0.52$	F(2, 131) = 0.80, $p = 0.45$	F(2, 131) = 0.64, $p = 0.53$
LI with same-sex stimuli	F(2, 132) = 0.05, $p = 0.82$	F(2, 132) = 0.72, $p = 0.49$	F(2, 132) = 0.71, $p = 0.49$
ALI with same-sex stimuli	F(2, 132) = 0.39, $p = 0.53$	F(2, 132) = 0.53, $p = 0.59$	F(2, 132) = 0.55, $p = 0.58$
LI with opposite-sex stimuli	F(2, 131) = 0.12, $p = 0.73$	F(2, 131) = 0.34, $p = 0.72$	F(2, 131) = 0.33, $p = 0.72$
ALI with opposite-sex stimuli	F(2, 131) = 0.11, $p = 0.74$	F(2, 131) = 0.97, $p = 0.38$	F(2, 131) = 0.06, $p = 0.94$

Table S.5. (continued)

	Main Effect	Sex/Color Morph	Interaction
Number of bites vs.			
LI in the mirror octagon	F(2, 134) = 0.49, p = 0.49	F(2, 134) = 0.48, p = 0.62	F(2, 134) = 0.12, p = 0.89
ALI in the mirror octagon	F(2, 134) = 0.17, p = 0.68	F(2, 134) = 3.55, p = 0.03	F(2, 134) = 0.68, p = 0.51
LI with male stimuli	F(2, 132) = 0.38, p = 0.54	F(2, 132) = 0.31, p = 0.74	F(2, 132) = 0.04, p = 0.96
ALI with male stimuli	F(2, 132) = 1.57, p = 0.21	F(2, 132) = 2.59, p = 0.08	F(2, 132) = 1.56, p = 0.21
LI with female stimuli	F(2, 131) = 0.11, p = 0.74	F(2, 131) = 0.98, p = 0.38	F(2, 131) = 0.76, p = 0.47
ALI with female stimuli	F(2, 131) = 0.09, p = 0.77	F(2, 131) = 4.31, p = 0.02	F(2, 131) = 1.40, p = 0.25
LI with same-sex stimuli	F(2, 132) = 0.09, p = 0.77	F(2, 132) = 0.25, p = 0.78	F(2, 132) = 0.06, p = 0.94
ALI with same-sex stimuli	F(2, 132) = 0.08, p = 0.78	F(2, 132) = 3.49, p = 0.03	F(2, 132) = 0.13, p = 0.88
LI with opposite-sex stimuli	F(2, 131) = 0.46, p = 0.50	F(2, 131) = 0.57, p = 0.56	F(2, 131) = 0.84, p = 0.44
ALI with opposite-sex stimuli	F(2, 131) = 1.72, p = 0.19	F(2, 131) = 3.55, p = 0.03	F(2, 131) = 2.60, p = 0.08
Number of charges vs.			
LI in the mirror octagon	F(2, 134) = 1.00, p = 0.32	F(2, 134) = 0.52, p = 0.60	F(2, 134) = 0.23, p = 0.80
ALI in the mirror octagon	F(2, 134) = 1.97, p = 0.16	F(2, 134) = 4.71, p = 0.01	F(2, 134) = 2.05, p = 0.13
LI with male stimuli	F(2, 132) = 0.97, p = 0.33	F(2, 132) = 0.43, p = 0.65	F(2, 132) = 1.03, p = 0.36
ALI with male stimuli	F(2, 132) = 0.01, p = 0.93	F(2, 132) = 2.45, p = 0.09	F(2, 132) = 0.23, p = 0.79
LI with female stimuli	F(2, 131) = 0.12, p = 0.73	F(2, 131) = 0.32, p = 0.73	F(2, 131) = 0.02, p = 0.98
ALI with female stimuli	F(2, 131) = 0.20, p = 0.65	F(2, 131) = 4.17, p = 0.02	F(2, 131) = 1.09, p = 0.34
LI with same-sex stimuli	F(2, 132) = 0.10, p = 0.75	F(2, 132) = 0.56, p = 0.57	F(2, 132) = 0.59, p = 0.55
ALI with same-sex stimuli	F(2, 132) = 0.19, p = 0.67	F(2, 132) = 4.93, p = 0.01	F(2, 132) = 0.52, p = 0.59
LI with opposite-sex stimuli	F(2, 131) = 1.14, p = 0.29	F(2, 131) = 0.13, p = 0.88	F(2, 131) = 0.30, p = 0.74
ALI with opposite-sex stimuli	F(2, 131) = 0.01, p = 0.93	F(2, 131) = 3.28, p = 0.04	F(2, 131) = 0.85, p = 0.43

Table S.5. (continued)

	Main Effect	Sex/Color Morph	Interaction
Number of lateral displays vs.			
LI in the mirror octagon	F(2, 134) = 1.28, p = 0.26	F(2, 134) = 0.24, p = 0.79	F(2, 134) = 0.05, p = 0.95
ALI in the mirror octagon	F(2, 134) = 0.61, p = 0.44	F(2, 134) = 2.17, p = 0.12	F(2, 134) = 0.13, p = 0.88
LI with male stimuli	F(2, 132) = 0.44, p = 0.51	F(2, 132) = 0.33, p = 0.72	F(2, 132) = 0.09, p = 0.91
ALI with male stimuli	F(2, 132) = 0.00, p = 0.96	F(2, 132) = 1.59, p = 0.21	F(2, 132) = 0.21, p = 0.81
LI with female stimuli	F(2, 131) = 0.29, p = 0.59	F(2, 131) = 0.21, p = 0.81	F(2, 131) = 0.32, p = 0.72
ALI with female stimuli	F(2, 131) = 0.15, p = 0.70	F(2, 131) = 2.79, p = 0.07	F(2, 131) = 0.17, p = 0.84
LI with same-sex stimuli	F(2, 132) = 0.24, p = 0.63	F(2, 132) = 0.32, p = 0.73	F(2, 132) = 0.64, p = 0.53
ALI with same-sex stimuli	F(2, 132) = 0.14, p = 0.71	F(2, 132) = 3.42, p = 0.04	F(2, 132) = 0.19, p = 0.83
LI with opposite-sex stimuli	F(2, 131) = 0.52, p = 0.47	F(2, 131) = 0.13, p = 0.88	F(2, 131) = 0.14, p = 0.87
ALI with opposite-sex stimuli	F(2, 131) = 0.00, p = 0.96	F(2, 131) = 2.02, p = 0.14	F(2, 131) = 0.28, p = 0.76
Number of tail beats vs.			
LI in the mirror octagon	F(2, 134) = 0.08, p = 0.78	F(2, 134) = 0.22, p = 0.80	F(2, 134) = 0.04, p = 0.96
ALI in the mirror octagon	F(2, 134) = 0.64, p = 0.42	F(2, 134) = 4.10, p = 0.02	F(2, 134) = 0.60, p = 0.55
LI with male stimuli	F(2, 132) = 2.87, p = 0.09	F(2, 132) = 0.58, p = 0.56	F(2, 132) = 1.15, p = 0.32
ALI with male stimuli	F(2, 132) = 1.98, p = 0.16	F(2, 132) = 3.01, p = 0.05	F(2, 132) = 2.36, p = 0.10
LI with female stimuli	F(2, 131) = 3.64, p = 0.06	F(2, 131) = 0.13, p = 0.88	F(2, 131) = 1.52, p = 0.22
ALI with female stimuli	F(2, 131) = 3.15, p = 0.08	F(2, 131) = 4.54, p = 0.01	F(2, 131) = 2.95, p = 0.06
LI with same-sex stimuli	F(2, 132) = 3.01, p = 0.09	F(2, 132) = 0.44, p = 0.65	F(2, 132) = 1.23, p = 0.30
ALI with same-sex stimuli	F(2, 132) = 2.90, p = 0.09	F(2, 132) = 6.44, p = 0.002	F(2, 132) = 3.07, p = 0.0501
LI with opposite-sex stimuli	F(2, 131) = 3.39, p = 0.07	F(2, 131) = 0.01, p = 0.99	F(2, 131) = 1.41, p = 0.25
ALI with opposite-sex stimuli	F(2, 131) = 2.13, p = 0.15	F(2, 131) = 2.97, p = 0.05	F(2, 131) = 2.30, p = 0.10

Table S.5. **(**continued)

	Main Effect	Sex/Color Morph	Interaction
Duration of bites vs.			
LI in the mirror octagon	F(2, 134) = 0.57, p = 0.45	F(2, 134) = 0.60, p = 0.55	F(2, 134) = 0.18, p = 0.83
ALI in the mirror octagon	F(2, 134) = 0.14, p = 0.71	F(2, 134) = 3.27, p = 0.04	F(2, 134) = 0.44, p = 0.64
LI with male stimuli	F(2, 132) = 0.14, p = 0.71	F(2, 132) = 0.37, p = 0.69	F(2, 132) = 0.07, p = 0.94
ALI with male stimuli	F(2, 132) = 0.57, p = 0.45	F(2, 132) = 2.60, p = 0.08	F(2, 132) = 0.99, p = 0.37
LI with female stimuli	F(2, 131) = 0.14, p = 0.71	F(2, 131) = 1.20, p = 0.31	F(2, 131) = 0.97, p = 0.38
ALI with female stimuli	F(2, 131) = 0.32, p = 0.57	F(2, 131) = 4.20, p = 0.02	F(2, 131) = 1.22, p = 0.30
LI with same-sex stimuli	F(2, 132) = 0.12, p = 0.73	F(2, 132) = 0.27, p = 0.77	F(2, 132) = 0.08, p = 0.93
ALI with same-sex stimuli	F(2, 132) = 0.29, p = 0.59	F(2, 132) = 3.72, p = 0.03	F(2, 132) = 0.05, p = 0.95
LI with opposite-sex stimuli	F(2, 131) = 0.17, p = 0.68	F(2, 131) = 0.59, p = 0.55	F(2, 131) = 0.87, p = 0.42
ALI with opposite-sex stimuli	F(2, 131) = 0.63, p = 0.43	F(2, 131) = 3.38, p = 0.04	F(2, 131) = 1.92, p = 0.15
Duration of charges vs.			
LI in the mirror octagon	F(2, 134) = 0.30, p = 0.58	F(2, 134) = 0.58, p = 0.56	F(2, 134) = 0.39, p = 0.68
ALI in the mirror octagon	F(2, 134) = 2.25, p = 0.14	F(2, 134) = 3.99, p = 0.02	F(2, 134) = 1.16, p = 0.32
LI with male stimuli	F(2, 132) = 0.05, p = 0.82	F(2, 132) = 0.35, p = 0.70	F(2, 132) = 0.08, p = 0.92
ALI with male stimuli	F(2, 132) = 0.19, p = 0.67	F(2, 132) = 2.11, p = 0.13	F(2, 132) = 0.11, p = 0.90
LI with female stimuli	F(2, 131) = 0.00, p = 1.00	F(2, 131) = 0.24, p = 0.78	F(2, 131) = 0.02, p = 0.98
ALI with female stimuli	F(2, 131) = 0.04, p = 0.85	F(2, 131) = 3.45, p = 0.03	F(2, 131) = 0.50, p = 0.61
LI with same-sex stimuli	F(2, 132) = 0.00, p = 1.00	F(2, 132) = 0.25, p = 0.78	F(2, 132) = 0.11, p = 0.89
ALI with same-sex stimuli	F(2, 132) = 0.03, p = 0.86	F(2, 132) = 4.31, p = 0.02	F(2, 132) = 0.23, p = 0.80
LI with opposite-sex stimuli	F(2, 131) = 0.06, p = 0.80	F(2, 131) = 0.02, p = 0.98	F(2, 131) = 0.00, p = 1.00
ALI with opposite-sex stimuli	F(2, 131) = 0.20, p = 0.65	F(2, 131) = 2.89, p = 0.06	F(2, 131) = 0.43, p = 0.65

Table S.5. (continued)

	Main Effect	**Sex/Color Morph**	**Interaction**
Duration of lateral displays vs.			
LI in the mirror octagon	F(2, 134) = 0.00, *p* = 0.97	F(2, 134) = 0.69, *p* = 0.50	F(2, 134) = 0.71, *p* = 0.50
ALI in the mirror octagon	F(2, 134) = 1.86, *p* = 0.18	F(2, 134) = 3.72, *p* = 0.03	F(2, 134) = 1.01, *p* = 0.37
LI with male stimuli	F(2, 132) = 2.88, *p* = 0.09	F(2, 132) = 0.47, *p* = 0.63	F(2, 132) = 0.43, *p* = 0.65
ALI with male stimuli	F(2, 132) = 2.39, *p* = 0.12	F(2, 132) = 2.26, *p* = 0.11	F(2, 132) = 0.21, *p* = 0.81
LI with female stimuli	F(2, 131) = 0.87, *p* = 0.35	F(2, 131) = 0.18, *p* = 0.84	F(2, 131) = 0.88, *p* = 0.42
ALI with female stimuli	F(2, 131) = 0.00, *p* = 0.95	F(2, 131) = 2.56, *p* = 0.08	F(2, 131) = 0.02, *p* = 0.98
LI with same-sex stimuli	F(2, 132) = 0.72, *p* = 0.40	F(2, 132) = 0.47, *p* = 0.62	F(2, 132) = 0.93, *p* = 0.40
ALI with same-sex stimuli	F(2, 132) = 0.00, *p* = 0.95	F(2, 132) = 3.92, *p* = 0.02	F(2, 132) = 0.35, *p* = 0.71
LI with opposite-sex stimuli	F(2, 131) = 3.41, *p* = 0.07	F(2, 131) = 0.09, *p* = 0.91	F(2, 131) = 0.06, *p* = 0.94
ALI with opposite-sex stimuli	F(2, 131) = 2.58, *p* = 0.11	F(2, 131) = 2.03, *p* = 0.14	F(2, 131) = 0.56, *p* = 0.57
Duration of tail beats vs.			
LI in the mirror octagon	F(2, 134) = 0.10, *p* = 0.75	F(2, 134) = 0.24, *p* = 0.79	F(2, 134) = 0.03, *p* = 0.97
ALI in the mirror octagon	F(2, 134) = 0.85, *p* = 0.36	F(2, 134) = 4.01, *p* = 0.02	F(2, 134) = 0.49, *p* = 0.61
LI with male stimuli	F(2, 132) = 3.22, *p* = 0.08	F(2, 132) = 0.61, *p* = 0.54	F(2, 132) = 1.22, *p* = 0.30
ALI with male stimuli	F(2, 132) = 1.63, *p* = 0.20	F(2, 132) = 3.25, *p* = 0.04	F(2, 132) = 2.20, *p* = 0.11
LI with female stimuli	F(2, 131) = 3.29, *p* = 0.07	F(2, 131) = 0.17, *p* = 0.85	F(2, 131) = 1.40, *p* = 0.25
ALI with female stimuli	F(2, 131) = 2.66, *p* = 0.11	F(2, 131) = 4.13, *p* = 0.02	F(2, 131) = 2.41, *p* = 0.09
LI with same-sex stimuli	F(2, 132) = 2.71, *p* = 0.10	F(2, 132) = 0.37, *p* = 0.69	F(2, 132) = 1.06, *p* = 0.35
ALI with same-sex stimuli	F(2, 132) = 2.48, *p* = 0.12	F(2, 132) = 6.77, *p* = 0.002	F(2, 132) = 2.92, *p* = 0.06
LI with opposite-sex stimuli	F(2, 131) = 3.81, *p* = 0.053	F(2, 131) = 0.01, *p* = 0.99	F(2, 131) = 1.60, *p* = 0.21
ALI with opposite-sex stimuli	F(2, 131) = 1.74, *p* = 0.19	F(2, 131) = 2.72, *p* = 0.07	F(2, 131) = 1.79, *p* = 0.17

Table S.6. Relationships between Boldness and LI and ALI measures.

	Main Effect	**Sex/Color Morph**	**Interaction**
Time spent "freaking-out" vs.			
LI in the mirror octagon	F(2, 133) = 1.02, p = 0.31	F(2, 133) = 0.76, p = 0.47	F(2, 133) = 2.03, p = 0.14
ALI in the mirror octagon	F(2, 133) = 4.09, p = 0.045	F(2, 133) = 1.80, p = 0.17	F(2, 133) = 1.35, p = 0.26
LI with male stimuli	F(2, 132) = 0.64, p = 0.43	F(2, 132) = 0.51, p = 0.60	F(2, 132) = 0.26, p = 0.77
ALI with male stimuli	F(2, 132) = 0.21, p = 0.65	F(2, 132) = 1.53, p = 0.22	F(2, 132) = 0.25, p = 0.78
LI with female stimuli	F(2, 131) = 1.24, p = 0.27	F(2, 131) = 0.07, p = 0.94	F(2, 131) = 0.21, p = 0.81
ALI with female stimuli	F(2, 131) = 0.01, p = 0.93	F(2, 131) = 0.87, p = 0.42	F(2, 131) = 1.02, p = 0.36
LI with same-sex stimuli	F(2, 132) = 1.03, p = 0.31	F(2, 132) = 0.44, p = 0.65	F(2, 132) = 0.35, p = 0.71
ALI with same-sex stimuli	F(2, 132) = 0.01, p = 0.93	F(2, 132) = 2.31, p = 0.10	F(2, 132) = 0.15, p = 0.87
LI with opposite-sex stimuli	F(2, 131) = 0.75, p = 0.39	F(2, 131) = 0.00, p = 1.00	F(2, 131) = 0.11, p = 0.90
ALI with opposite-sex stimuli	F(2, 131) = 0.24, p = 0.63	F(2, 131) = 2.06, p = 0.13	F(2, 131) = 1.34, p = 0.27
Number of squares entered during "the freak-out period" vs.			
LI in the mirror octagon	F(2, 133) = 0.77, p = 0.38	F(2, 133) = 0.60, p = 0.55	F(2, 133) = 1.63, p = 0.20
ALI in the mirror octagon	F(2, 133) = 2.87, p = 0.09	F(2, 133) = 1.90, p = 0.15	F(2, 133) = 1.09, p = 0.34
LI with male stimuli	F(2, 132) = 0.50, p = 0.48	F(2, 132) = 0.50, p = 0.61	F(2, 132) = 0.21, p = 0.81
ALI with male stimuli	F(2, 132) = 0.09, p = 0.76	F(2, 132) = 1.87, p = 0.16	F(2, 132) = 0.07, p = 0.93
LI with female stimuli	F(2, 131) = 0.33, p = 0.57	F(2, 131) = 0.13, p = 0.87	F(2, 131) = 0.13, p = 0.88
ALI with female stimuli	F(2, 131) = 0.00, p = 0.95	F(2, 131) = 1.10, = 0.34	F(2, 131) = 0.70, p = 0.50
LI with same-sex stimuli	F(2, 132) = 0.27, p = 0.60	F(2, 132) = 0.36, p = 0.70	F(2, 132) = 0.18, p = 0.83
ALI with same-sex stimuli	F(2, 132) = 0.00, p = 0.95	F(2, 132) = 2.93, p = 0.06	F(2, 132) = 0.04, p = 0.96
LI with opposite-sex stimuli	F(2, 131) = 0.59, p = 0.44	F(2, 131) = 0.01, p = 0.99	F(2, 131) = 0.21, p = 0.81
ALI with opposite-sex stimuli	F(2, 131) = 0.10, p = 0.75	F(2, 131) = 2.01, p = 0.14	F(2, 131) = 0.86, p = 0.42

Table S.6. (continued)

	Main Effect	**Sex/Color Morph**	**Interaction**
Total number of squares entered vs.			
LI in the mirror octagon	F(2, 133) = 0.02, *p* = 0.88	F(2, 133) = 1.07, *p* = 0.35	F(2, 133) = 0.94, *p* = 0.39
ALI in the mirror octagon	F(2, 133) = 5.12, *p* = 0.03	F(2, 133) = 6.52, *p* = 0.002	F(2, 133) = 1.79, *p* = 0.17
LI with male stimuli	F(2, 132) = 0.18, *p* = 0.67	F(2, 132) = 0.31, *p* = 0.74	F(2, 132) = 0.47, *p* = 0.63
ALI with male stimuli	F(2, 132) = 0.30, *p* = 0.59	F(2, 132) = 4.41, *p* = 0.01	F(2, 132) = 1.39, *p* = 0.25
LI with female stimuli	F(2, 131) = 0.27, *p* = 0.61	F(2, 131) = 0.07, *p* = 0.93	F(2, 131) = 0.19, *p* = 0.82
ALI with female stimuli	F(2, 131) = 0.03, *p* = 0.85	F(2, 131) = 4.23, *p* = 0.02	F(2, 131) = 1.19, *p* = 0.31
LI with same-sex stimuli	F(2, 132) = 0.22, *p* = 0.64	F(2, 132) = 0.31, *p* = 0.73	F(2, 132) = 0.10, *p* = 0.90
ALI with same-sex stimuli	F(2, 132) = 0.03, *p* = 0.86	F(2, 132) = 5.86, *p* = 0.00	F(2, 132) = 0.90, *p* = 0.41
LI with opposite-sex stimuli	F(2, 131) = 0.21, *p* = 0.65	F(2, 131) = 0.10, *p* = 0.91	F(2, 131) = 0.06, *p* = 0.94
ALI with opposite-sex stimuli	F(2, 131) = 0.32, *p* = 0.57	F(2, 131) = 3.44, *p* = 0.04	F(2, 131) = 1.48, *p* = 0.23
Proportion of corner squares entered vs.			
LI in the mirror octagon	F(2, 133) = 0.09, *p* = 0.77	F(2, 133) = 0.27, *p* = 0.77	F(2, 133) = 0.17, *p* = 0.84
ALI in the mirror octagon	F(2, 133) = 0.00, *p* = 1.00	F(2, 133) = 0.65, *p* = 0.52	F(2, 133) = 0.02, *p* = 0.98
LI with male stimuli	F(2, 132) = 0.32, *p* = 0.57	F(2, 132) = 1.08, *p* = 0.34	F(2, 132) = 1.09, *p* = 0.34
ALI with male stimuli	F(2, 132) = 0.07, *p* = 0.79	F(2, 132) = 0.08, *p* = 0.92	F(2, 132) = 0.33, *p* = 0.72
LI with female stimuli	F(2, 131) = 1.05, *p* = 0.31	F(2, 131) = 0.12, *p* = 0.89	F(2, 131) = 0.02, *p* = 0.98
ALI with female stimuli	F(2, 131) = 0.03, *p* = 0.87	F(2, 131) = 0.17, *p* = 0.84	F(2, 131) = 1.38, *p* = 0.26
LI with same-sex stimuli	F(2, 132) = 0.87, *p* = 0.35	F(2, 132) = 0.04, *p* = 0.96	F(2, 132) = 0.06, *p* = 0.94
ALI with same-sex stimuli	F(2, 132) = 0.02, *p* = 0.88	F(2, 132) = 0.26, *p* = 0.77	F(2, 132) = 0.44, *p* = 0.65
LI with opposite-sex stimuli	F(2, 131) = 0.37, *p* = 0.54	F(2, 131) = 0.44, *p* = 0.65	F(2, 131) = 0.90, *p* = 0.41
ALI with opposite-sex stimuli	F(2, 131) = 0.08, *p* = 0.78	F(2, 131) = 0.90, *p* = 0.41	F(2, 131) = 1.09, *p* = 0.34

Table S.6. (continued)

	Main Effect	**Sex/Color Morph**	**Interaction**
Proportion of middle squares entered vs.			
LI in the mirror octagon	F(2, 133) = 4.56, $p = 0.03$	F(2, 133) = 0.49, $p = 0.62$	F(2, 133) = 2.81, $p = 0.06$
ALI in the mirror octagon	F(2, 133) = 4.34, $p = 0.04$	F(2, 133) = 3.28, $p = 0.04$	F(2, 133) = 0.76, $p = 0.47$
LI with male stimuli	F(2, 132) = 0.25, $p = 0.62$	F(2, 132) = 0.14, $p = 0.87$	F(2, 132) = 0.01, $p = 0.99$
ALI with male stimuli	F(2, 132) = 0.51, $p = 0.48$	F(2, 132) = 3.55, $p = 0.03$	F(2, 132) = 0.21, $p = 0.81$
LI with female stimuli	F(2, 131) = 1.84, $p = 0.18$	F(2, 131) = 0.08, $p = 0.93$	F(2, 131) = 0.47, $p = 0.63$
ALI with female stimuli	F(2, 131) = 0.96, $p = 0.33$	F(2, 131) = 3.88, $p = 0.02$	F(2, 131) = 1.09, $p = 0.34$
LI with same-sex stimuli	F(2, 132) = 1.52, $p = 0.22$	F(2, 132) = 0.26, $p = 0.77$	F(2, 132) = 0.69, $p = 0.50$
ALI with same-sex stimuli	F(2, 132) = 0.88, $p = 0.35$	F(2, 132) = 5.08, $p = 0.01$	F(2, 132) = 0.26, $p = 0.77$
LI with opposite-sex stimuli	F(2, 131) = 0.30, $p = 0.59$	F(2, 131) = 0.15, $p = 0.86$	F(2, 131) = 0.10, $p = 0.90$
ALI with opposite-sex stimuli	F(2, 131) = 0.55, $p = 0.46$	F(2, 131) = 2.69, $p = 0.07$	F(2, 131) = 0.81, $p = 0.45$
Proportion of edge squares entered vs.			
LI in the mirror octagon	F(2, 133) = 5.31, $p = 0.02$	F(2, 133) = 2.26, $p = 0.11$	F(2, 133) = 1.97, $p = 0.14$
ALI in the mirror octagon	F(2, 133) = 4.24, $p = 0.04$	F(2, 133) = 1.20, $p = 0.31$	F(2, 133) = 0.73, $p = 0.48$
LI with male stimuli	F(2, 132) = 0.03, $p = 0.86$	F(2, 132) = 0.50, $p = 0.61$	F(2, 132) = 0.60, $p = 0.55$
ALI with male stimuli	F(2, 132) = 0.76, $p = 0.38$	F(2, 132) = 0.23, $p = 0.80$	F(2, 132) = 0.13, $p = 0.88$
LI with female stimuli	F(2, 131) = 0.57, $p = 0.45$	F(2, 131) = 1.15, $p = 0.32$	F(2, 131) = 0.84, $p = 0.43$
ALI with female stimuli	F(2, 131) = 1.14, $p = 0.29$	F(2, 131) = 0.23, $p = 0.79$	F(2, 131) = 0.05, $p = 0.96$
LI with same-sex stimuli	F(2, 132) = 0.47, $p = 0.49$	F(2, 132) = 1.58, $p = 0.21$	F(2, 132) = 1.58, $p = 0.21$
ALI with same-sex stimuli	F(2, 132) = 1.06, $p = 0.30$	F(2, 132) = 0.50, $p = 0.61$	F(2, 132) = 0.10, $p = 0.90$
LI with opposite-sex stimuli	F(2, 131) = 0.03, $p = 0.85$	F(2, 131) = 0.20, $p = 0.82$	F(2, 131) = 0.17, $p = 0.85$
ALI with opposite-sex stimuli	F(2, 131) = 0.81, $p = 0.37$	F(2, 131) = 0.21, $p = 0.81$	F(2, 131) = 0.04, $p = 0.97$

Table S.6. (continued)

	Main Effect	**Sex/Color Morph**	**Interaction**
Time spent in corner squares vs.			
LI in the mirror octagon	F(2, 133) = 2.23, *p* = 0.14	F(2, 133) = 0.04, *p* = 0.96	F(2, 133) = 0.42, *p* = 0.66
ALI in the mirror octagon	F(2, 133) = 0.33, *p* = 0.57	F(2, 133) = 2.77, *p* = 0.07	F(2, 133) = 0.18, *p* = 0.83
LI with male stimuli	F(2, 132) = 0.74, *p* = 0.39	F(2, 132) = 2.06, *p* = 0.13	F(2, 132) = 2.44, *p* = 0.09
ALI with male stimuli	F(2, 132) = 1.78, *p* = 0.18	F(2, 132) = 1.09, *p* = 0.34	F(2, 132) = 0.14, *p* = 0.87
LI with female stimuli	F(2, 131) = 0.16, *p* = 0.69	F(2, 131) = 0.16, *p* = 0.85	F(2, 131) = 0.01, *p* = 0.99
ALI with female stimuli	F(2, 131) = 0.11, *p* = 0.74	F(2, 131) = 0.40, *p* = 0.67	F(2, 131) = 0.50, *p* = 0.61
LI with same-sex stimuli	F(2, 132) = 0.14, *p* = 0.71	F(2, 132) = 0.51, *p* = 0.60	F(2, 132) = 1.12, *p* = 0.33
ALI with same-sex stimuli	F(2, 132) = 0.10, *p* = 0.75	F(2, 132) = 1.28, *p* = 0.28	F(2, 132) = 0.06, *p* = 0.94
LI with opposite-sex stimuli	F(2, 131) = 0.84, *p* = 0.36	F(2, 131) = 0.22, *p* = 0.80	F(2, 131) = 0.49, *p* = 0.62
ALI with opposite-sex stimuli	F(2, 131) = 1.96, *p* = 0.16	F(2, 131) = 0.41, *p* = 0.67	F(2, 131) = 0.19, *p* = 0.83
Time spent in edge squares vs.			
LI in the mirror octagon	F(2, 133) = 1.75, *p* = 0.19	F(2, 133) = 0.71, *p* = 0.50	F(2, 133) = 0.33, *p* = 0.72
ALI in the mirror octagon	F(2, 133) = 0.27, *p* = 0.60	F(2, 133) = 0.99, *p* = 0.38	F(2, 133) = 0.20, *p* = 0.82
LI with male stimuli	F(2, 132) = 0.80, *p* = 0.37	F(2, 132) = 1.53, *p* = 0.22	F(2, 132) = 2.63, *p* = 0.08
ALI with male stimuli	F(2, 132) = 1.52, *p* = 0.22	F(2, 132) = 1.48, *p* = 0.23	F(2, 132) = 0.08, *p* = 0.92
LI with female stimuli	F(2, 131) = 0.10, *p* = 0.76	F(2, 131) = 0.05, *p* = 0.95	F(2, 131) = 0.12, *p* = 0.89
ALI with female stimuli	F(2, 131) = 0.08, *p* = 0.78	F(2, 131) = 1.49, *p* = 0.23	F(2, 131) = 0.17, *p* = 0.84
LI with same-sex stimuli	F(2, 132) = 0.08, *p* = 0.77	F(2, 132) = 1.25, *p* = 0.29	F(2, 132) = 1.40, *p* = 0.25
ALI with same-sex stimuli	F(2, 132) = 0.07, *p* = 0.79	F(2, 132) = 2.31, *p* = 0.10	F(2, 132) = 0.10, *p* = 0.91
LI with opposite-sex stimuli	F(2, 131) = 0.90, *p* = 0.34	F(2, 131) = 0.19, *p* = 0.83	F(2, 131) = 0.17, *p* = 0.85
ALI with opposite-sex stimuli	F(2, 131) = 1.64, *p* = 0.20	F(2, 131) = 1.35, *p* = 0.26	F(2, 131) = 0.10, *p* = 0.91

Table S.6. (continued)

	Main Effect	Sex/Color Morph	Interaction
Time spent in middle squares vs.			
LI in the mirror octagon	F(2, 133) = 0.02, *p* = 0.88	F(2, 133) = 0.40, *p* = 0.67	F(2, 133) = 0.01, *p* = 0.99
ALI in the mirror octagon	F(2, 133) = 2.09, *p* = 0.15	F(2, 133) = 5.14, *p* = 0.01	F(2, 133) = 0.82, *p* = 0.44
LI with male stimuli	F(2, 132) = 0.35, *p* = 0.56	F(2, 132) = 0.28, *p* = 0.76	F(2, 132) = 0.13, *p* = 0.88
ALI with male stimuli	F(2, 132) = 0.19, *p* = 0.67	F(2, 132) = 3.46, *p* = 0.03	F(2, 132) = 0.23, *p* = 0.79
LI with female stimuli	F(2, 131) = 0.09, *p* = 0.76	F(2, 131) = 0.55, *p* = 0.58	F(2, 131) = 0.08, *p* = 0.92
ALI with female stimuli	F(2, 131) = 0.26, *p* = 0.61	F(2, 131) = 3.17, *p* = 0.05	F(2, 131) = 0.14, *p* = 0.87
LI with same-sex stimuli	F(2, 132) = 0.08, *p* = 0.78	F(2, 132) = 0.15, *p* = 0.86	F(2, 132) = 0.03, *p* = 0.97
ALI with same-sex stimuli	F(2, 132) = 0.24, *p* = 0.62	F(2, 132) = 4.66, *p* = 0.01	F(2, 132) = 0.28, *p* = 0.76
LI with opposite-sex stimuli	F(2, 131) = 0.41, *p* = 0.52	F(2, 131) = 0.08, *p* = 0.92	F(2, 131) = 0.17, *p* = 0.85
ALI with opposite-sex stimuli	F(2, 131) = 0.20, *p* = 0.65	F(2, 131) = 3.00, *p* = 0.05	F(2, 131) = 0.12, *p* = 0.89
Log time to emerge vs.			
LI in the mirror octagon	F(2, 133) = 0.63, *p* = 0.67	F(2, 133) = 0.20, *p* = 0.82	F(2, 133) = 0.40, *p* = 0.67
ALI in the mirror octagon	F(2, 133) = 1.02, *p* = 0.31	F(2, 133) = 0.34, *p* = 0.71	F(2, 133) = 0.29, *p* = 0.75
LI with male stimuli	F(2, 132) = 0.40, *p* = 0.53	F(2, 132) = 0.66, *p* = 0.52	F(2, 132) = 0.71, *p* = 0.49
ALI with male stimuli	F(2, 132) = 0.00, *p* = 1.00	F(2, 132) = 0.15, *p* = 0.86	F(2, 132) = 0.56, *p* = 0.57
LI with female stimuli	F(2, 131) = 0.17, *p* = 0.68	F(2, 131) = 0.01, *p* = 0.99	F(2, 131) = 0.05, *p* = 0.95
ALI with female stimuli	F(2, 131) = 1.56, *p* = 0.21	F(2, 131) = 0.52, *p* = 0.60	F(2, 131) = 2.35, *p* = 0.10
LI with same-sex stimuli	F(2, 132) = 0.14, *p* = 0.71	F(2, 132) = 0.63, *p* = 0.53	F(2, 132) = 0.46, *p* = 0.63
ALI with same-sex stimuli	F(2, 132) = 1.34, *p* = 0.25	F(2, 132) = 0.41, *p* = 0.67	F(2, 132) = 0.73, *p* = 0.49
LI with opposite-sex stimuli	F(2, 131) = 0.47, *p* = 0.49	F(2, 131) = 0.18, *p* = 0.83	F(2, 131) = 0.21, *p* = 0.81
ALI with opposite-sex stimuli	F(2, 131) = 0.00, *p* = 1.00	F(2, 131) = 1.52, *p* = 0.22	F(2, 131) = 2.74, *p* = 0.07

Table S.7. PCA loadings results of the mirror aggression outcome measures. Six components were identified in the PCA analysis the first four components accounted for 94.5% of the variance and are presented below.

	Component 1	**Component 2**	**Component 3**	**Component 4**
Cumulative Proportion of Variance	58.6%	73.8%	87.7%	94.5%
	Loadings			
Time to first aggressive action	0.484	0.191	-0.337	0.771
Number of bites	-0.484	-0.151	0.435	0.414
Number of charges	-0.494	0.346	0.132	0.411
Number of lateral displays	-0.359	-0.680	-0.611	0.148
Number of tail beats	-0.397	0.599	-0.553	-0.211

Table S.8. PCA loadings results of the open field outcome measures. Six components were identified in the PCA analysis the first four components accounted for 91.7% of the variance and are presented below.

	Component 1	**Component 2**	**Component 3**	**Component 4**
Cumulative Proportion of Variance	36.2%	69.4%	82.4%	91.7%
	Loadings			
Time spent in corner squares	-0.420	0.428	-0.111	0.381
Time spent in middle squares	-0.152	-0.468	-0.457	-0.120
Time spent in edge squares	0.524	-0.203	0.363	-0.316
Proportion of corner squares entered	-0.319	0.406	0.207	-0.664
Proportion of middle squares entered	0.520	0.251	-0.103	0.400
Proportion of edge squares entered	-0.296	-0.528		
Total number of squares entered	0.258	0.224	-0.769	-0.369

Table S.9. PCA loadings results of all the chosen outcome measures. Eight components were identified in the PCA analysis the first four components accounted for 66.1% of the variance and are presented below.

	Component 1	**Component 2**	**Component 3**	**Component 4**
Cumulative Proportion of Variance	31.0%	44.3%	55.9%	66.1%
	Loadings			
Aggression Principle Component 1	-0.110	0.553	0.137	0.206
Aggression Principle Component 2		0.216	0.435	0.219
Open Field Principle Component 1	0.182	-0.392		-0.561
Open Field Principle Component 2			0.700	-0.442
Log Time to Emerge	-0.156	0.550		-0.455
Mirror Octagon ALI	-0.225	0.293	-0.492	-0.325
Circular Lateralization with Male Stimuli ALI	-0.469	-0.233		0.171
Circular Lateralization with Female Stimuli ALI	-0.470		0.120	-0.140
Circular Lateralization with Same-sex Stimuli ALI	-0.464	-0.190		0.159
Circular Lateralization with Opposite-sex Stimuli ALI	-0.468	-0.101	0.178	-0.114

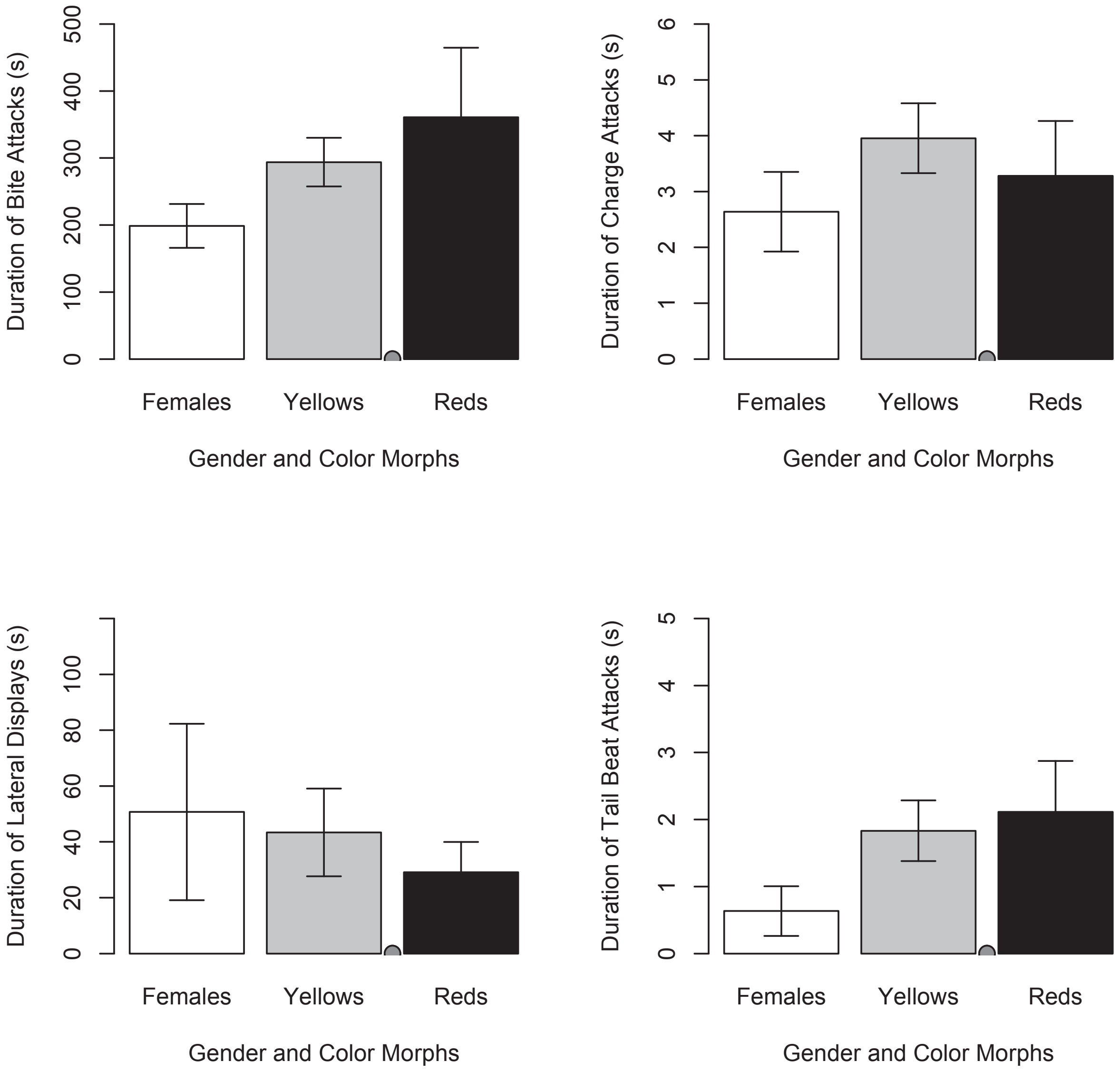

Figure S.1. Female and male color morph duration measures of specific aggressive behaviors in the mirror aggression task. Average (±SEM) duration per fish of bites (a), charges (b), lateral displays (c), and tail beats (d) at their mirror image for females (white bars), yellow morphs (gray bars), and red morphs (black bars). None of the groups differed significantly in the amount of time they spent performing the various actions.

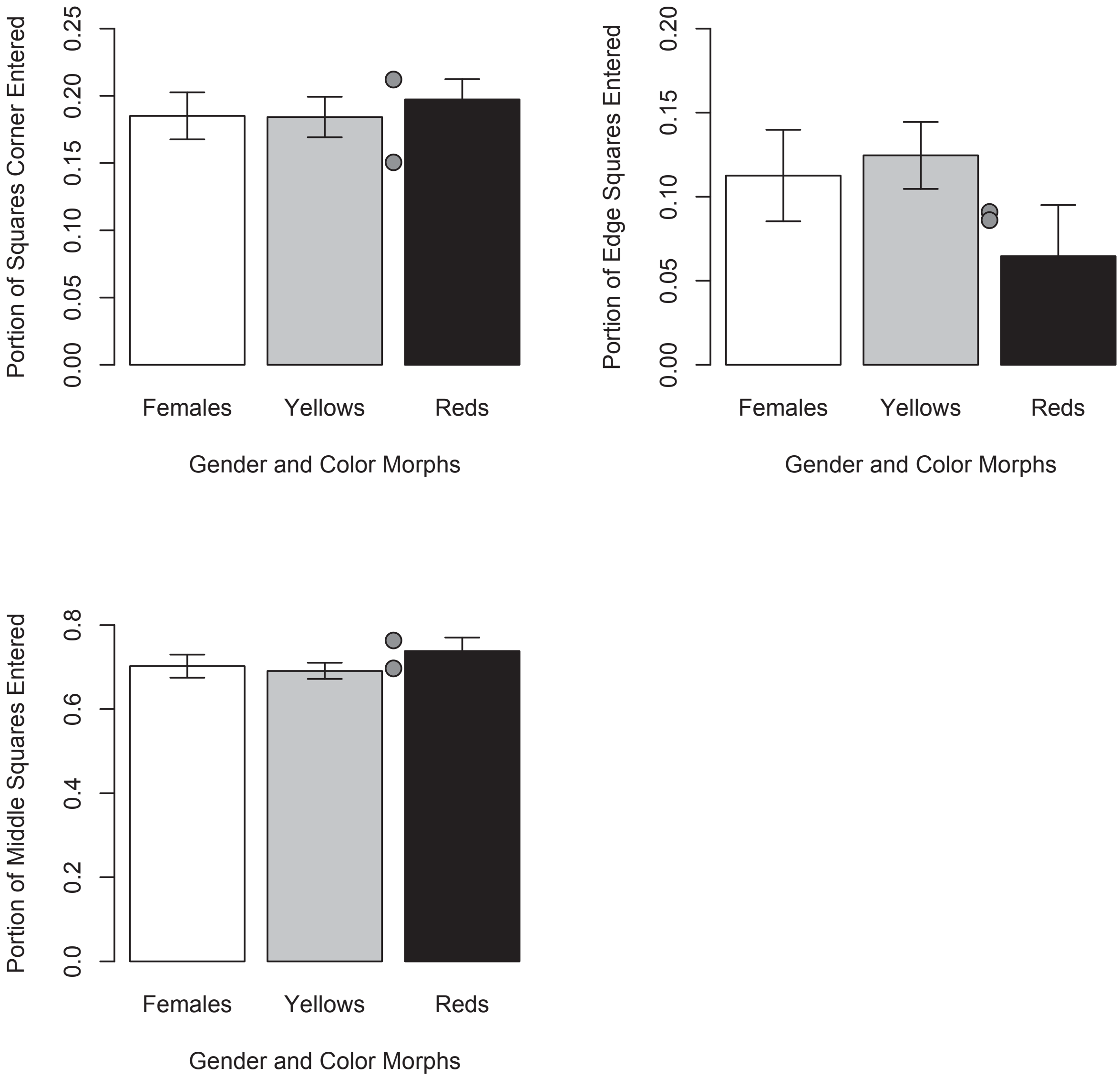

Figure S.2. Female and male color morph proportions of squares entered in the open field task. Average (±SEM) proportion of corner squares entered (b), proportion of edge squares entered (c), and proportion of middle squares entered (d) during the open field exploration task for females (white bars), yellow morphs (gray bars), and red morphs (black bars).

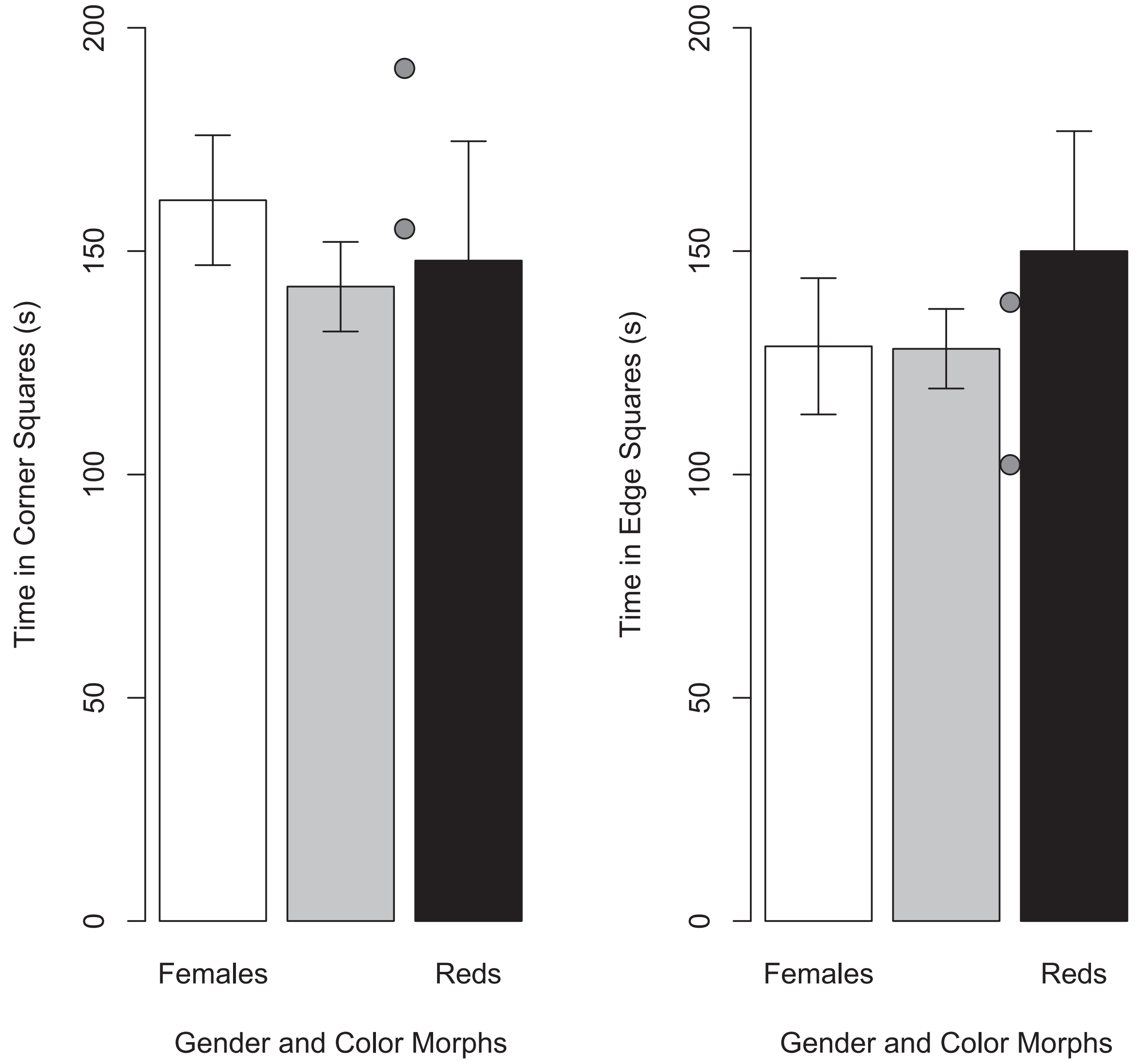

Figure S.3. Female and male color morph duration of time spent in corner and edge squares of the open field task. Average (±SEM) time spent in corner squares (a) and time spent in edge squares (b) during the open field exploration task. Females are indicated by white bar and dotted line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

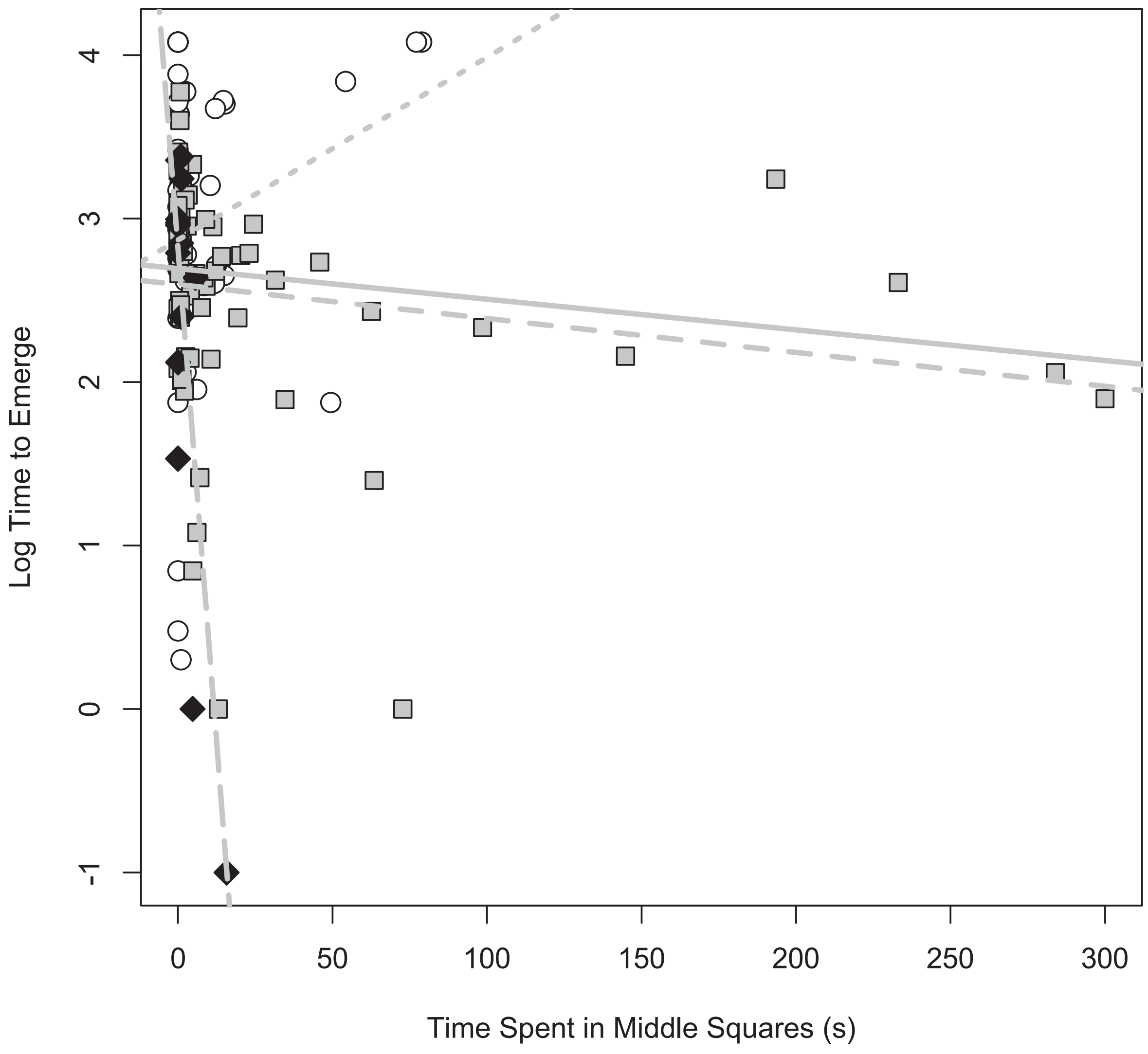

Figure S.4. The relationship between the time spent in middle squares in the open field task and the log transform of time to emerge in the novel environment task. The main effect of time spent in middle squares on the log transform of time to emerge trended towards significance (solid line; $p = 0.08$), while the interaction term with sex and color morph was significant ($p < 0.001$). Females are indicated by white circles and dotted line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

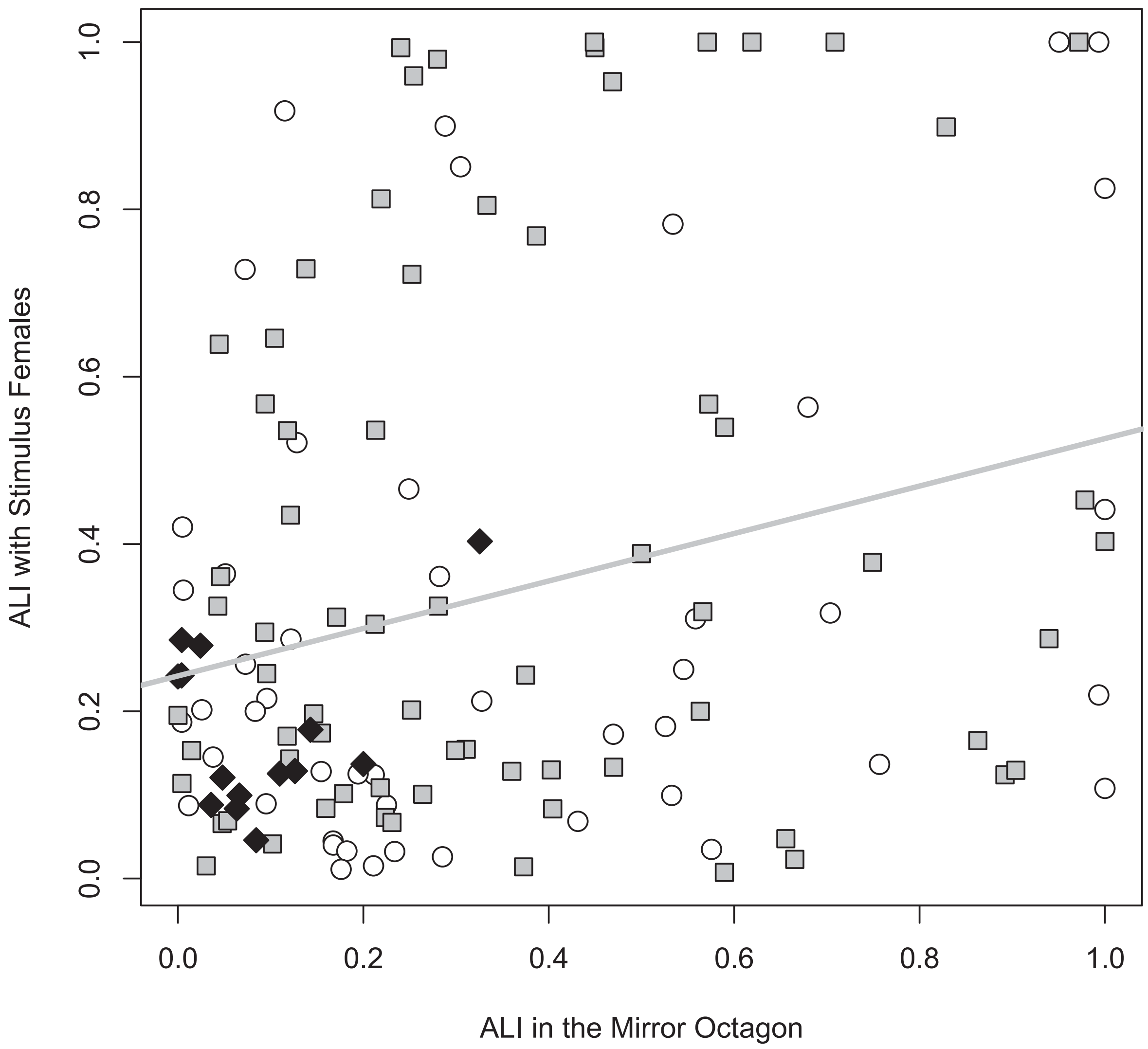

Figure S.5. The relationship between the absolute lateralization index (ALI) in the mirror octagon and the ALI from the circular lateralization task with female stimulus fish. The main effect of the ALI in the mirror octagon on ALI with female stimulus fish was found to be significant ($p = 0.04$), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; $p = 0.95$).

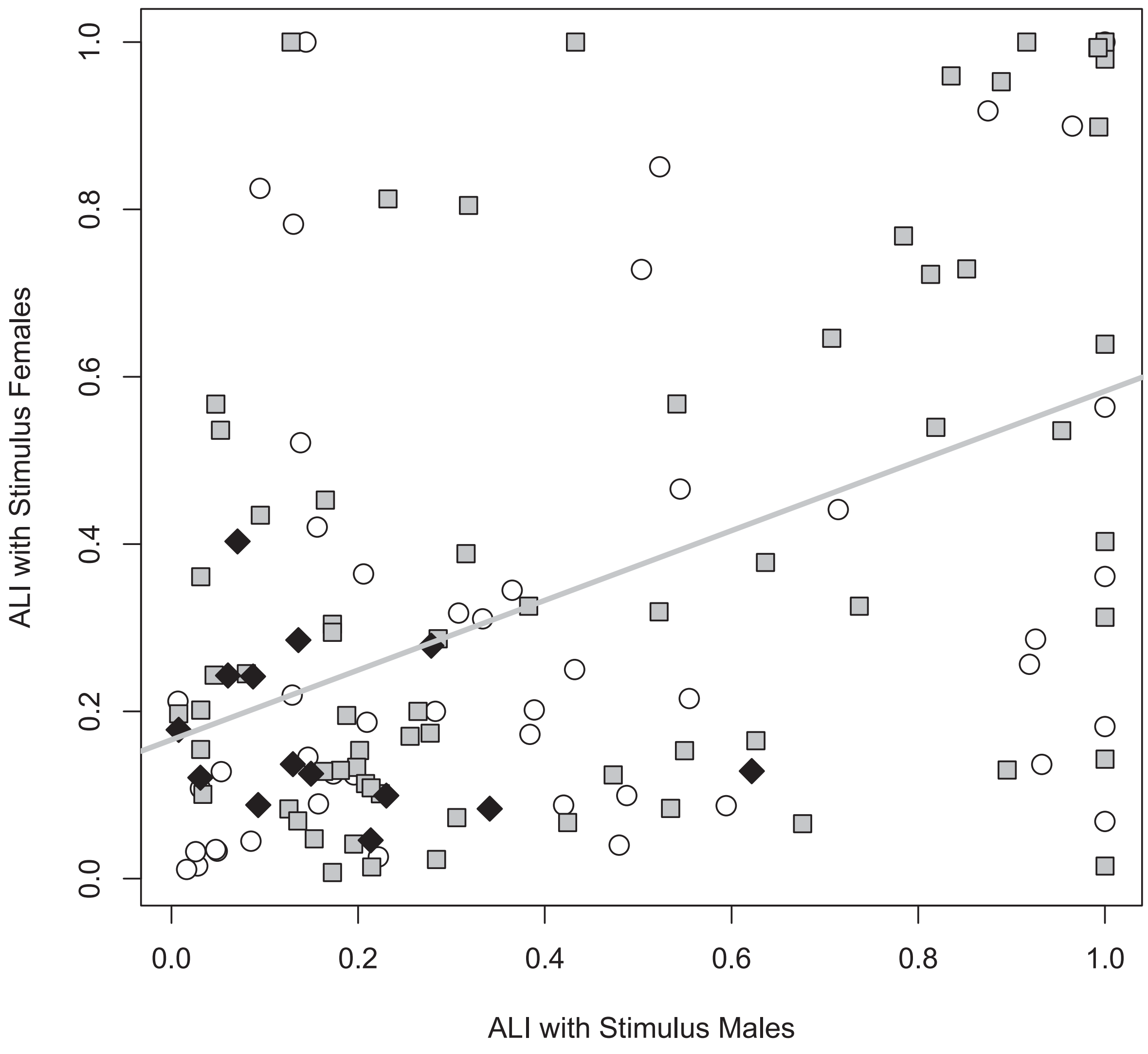

Figure S.6. The relationship between the absolute lateralization index (ALI) from the circular lateralization task with male stimuli and the ALI from the circular lateralization task with female stimulus fish. The main effect of the ALI with male stimuli on ALI with female stimulus fish was found to be significant ($p = 0.02$), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; $p = 0.16$).

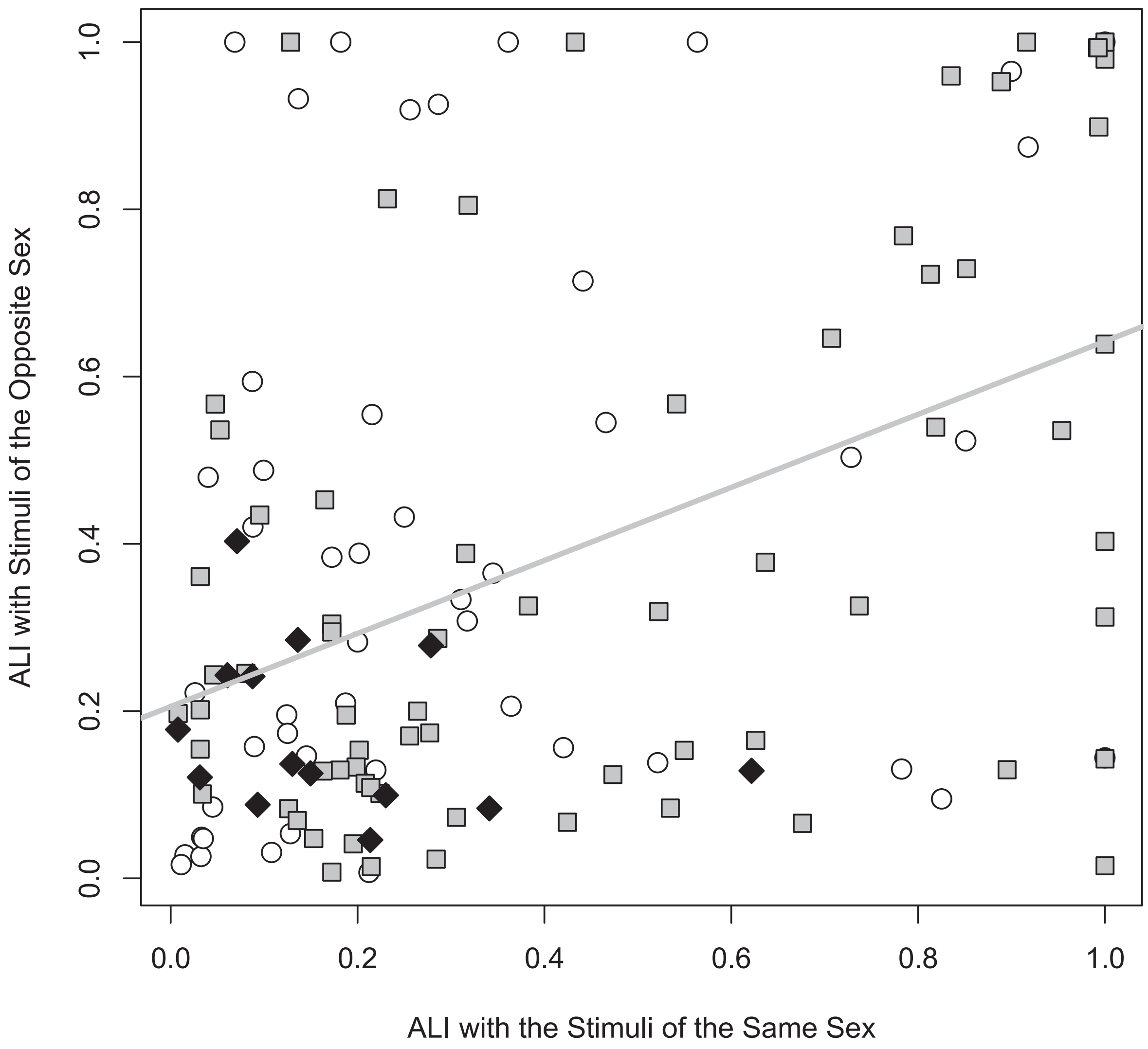

Figure S.7. The relationship between the absolute lateralization index (ALI) from the circular lateralization task with stimuli of the same sex and the ALI from the circular lateralization task with stimuli of the opposite sex. The main effect of the ALI with stimuli of the same sex on ALI with stimuli of the opposite sex was found to be significant (*p* = 0.01), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; *p* = 0.36).

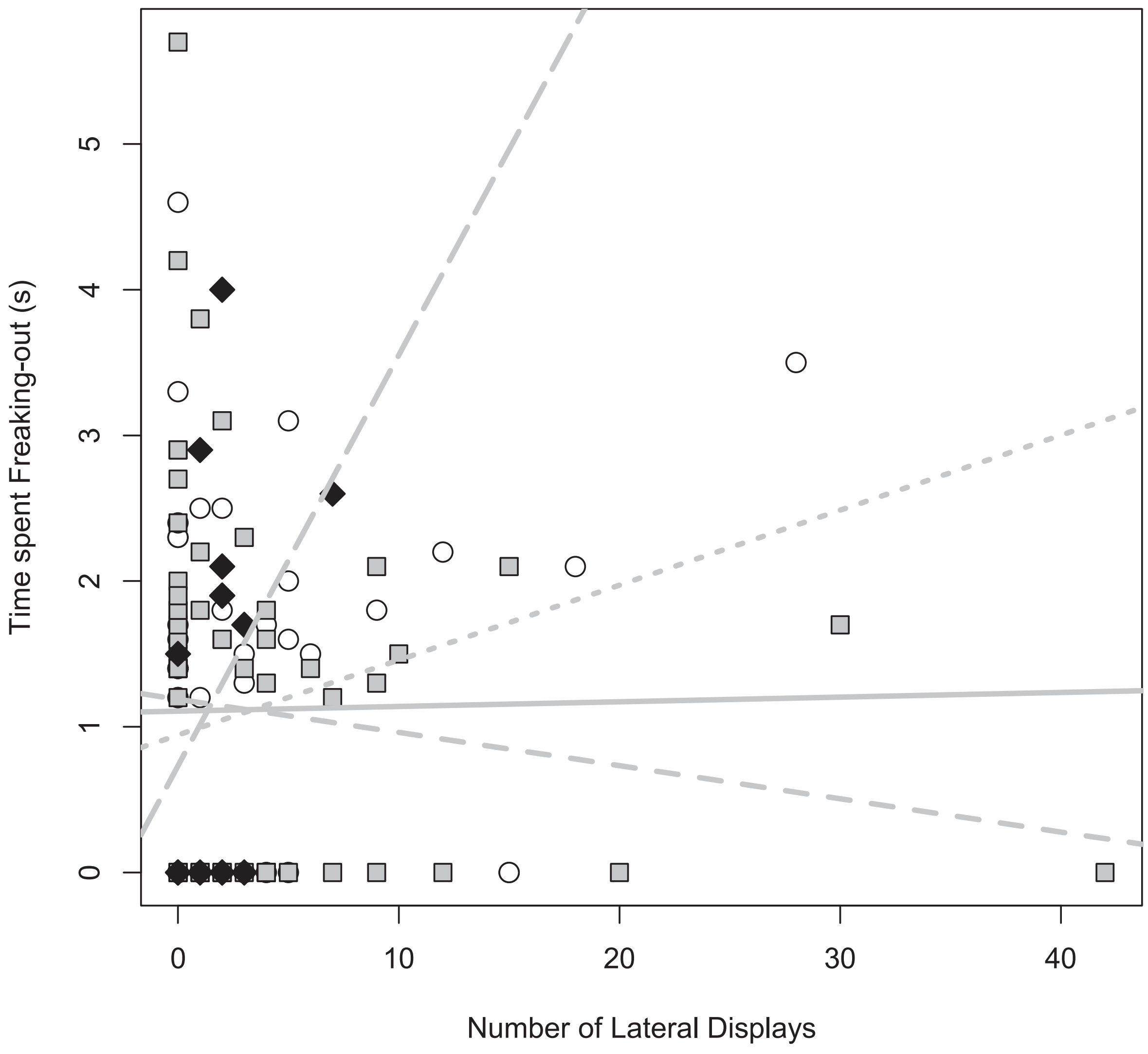

Figure S.8. The relationship between the number of lateral displays from the mirror aggression task and the time spent "freaking-out" during the open field task. The main effect of the number of lateral displays on the time spent "freaking-out" trended towards significance (solid line, *p* = 0.10), while the interaction term with sex and color morph was significant (*p* = 0.045). Females are indicated by white circles and dotted line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

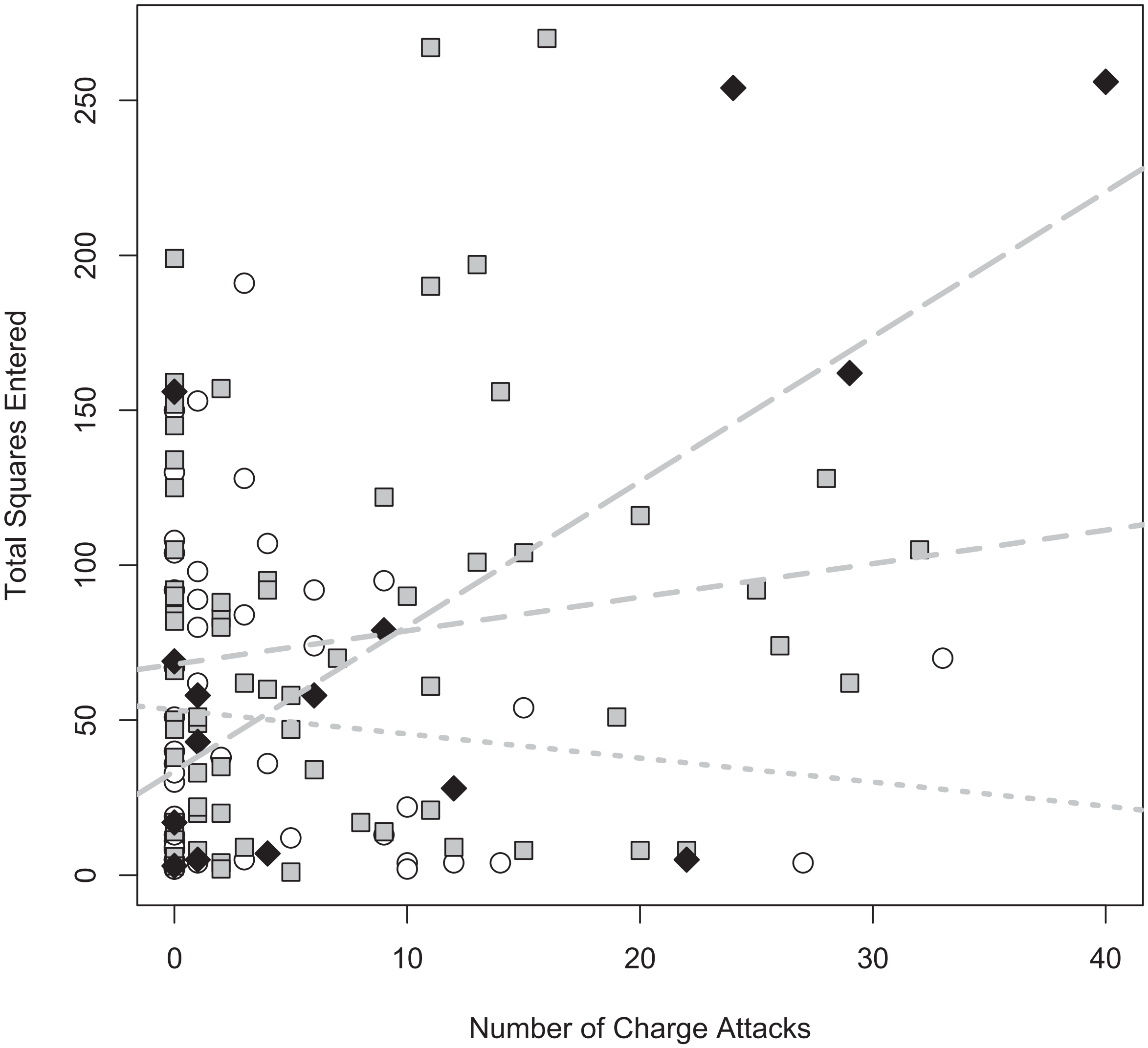

Figure S.9. The relationship between the number of charges from the mirror aggression task and the total number of squares entered during the open field task. The main effect of the number of charges on the total number of squares entered was not significant (*p* = 0.52), while the interaction term with sex and color morph was significant (*p* = 0.006). Females are indicated by white circles and dotted gray line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

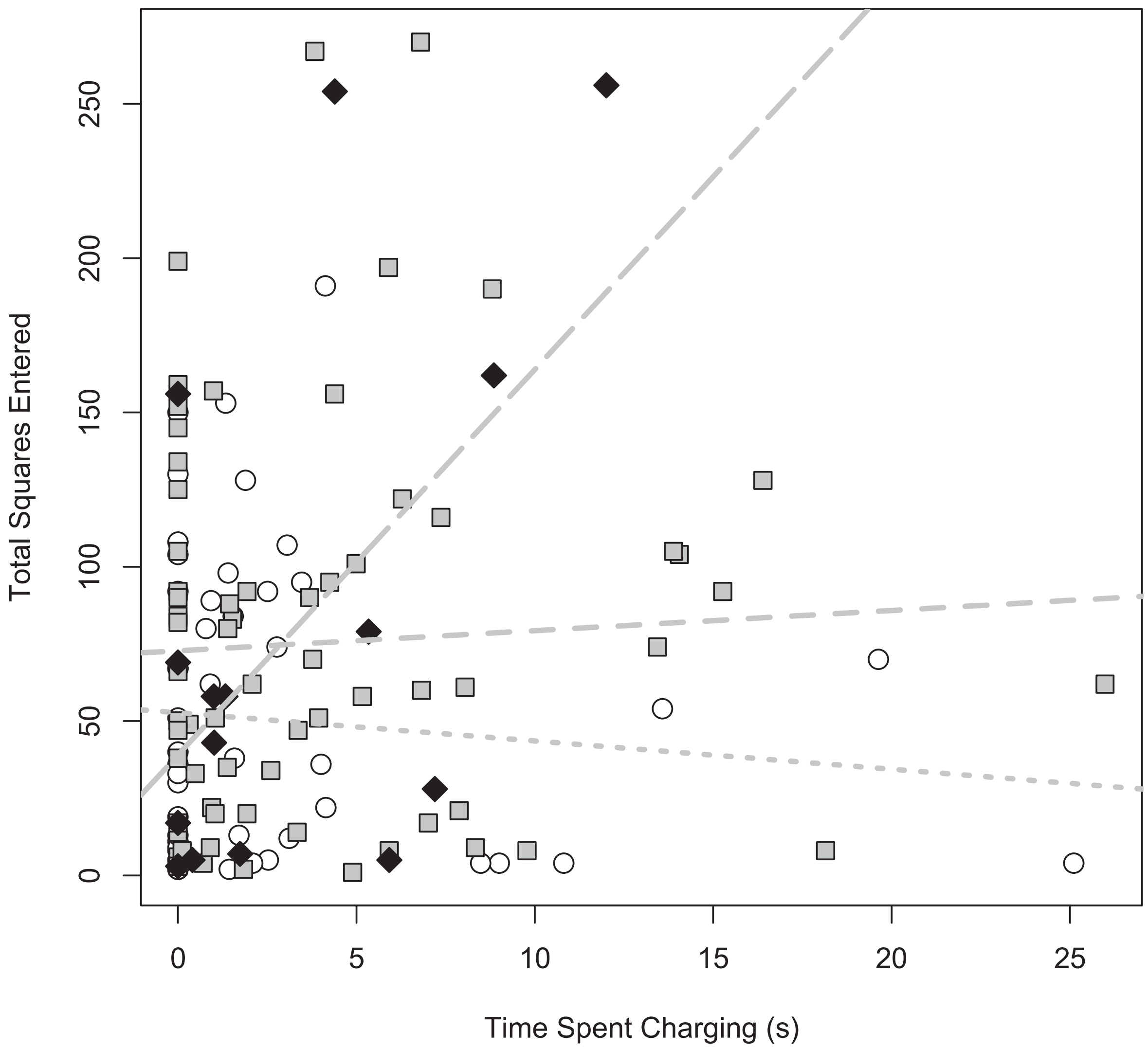

Figure S.10. The relationship between the time spent performing charges from the mirror aggression task and the total number of squares entered during the open field task. The main effect of the number of charges on the total number of squares entered was not significant (*p* = 0.59), while the interaction term with sex and color morph was significant (*p* = 0.01). Females are indicated by white circles and dotted gray line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

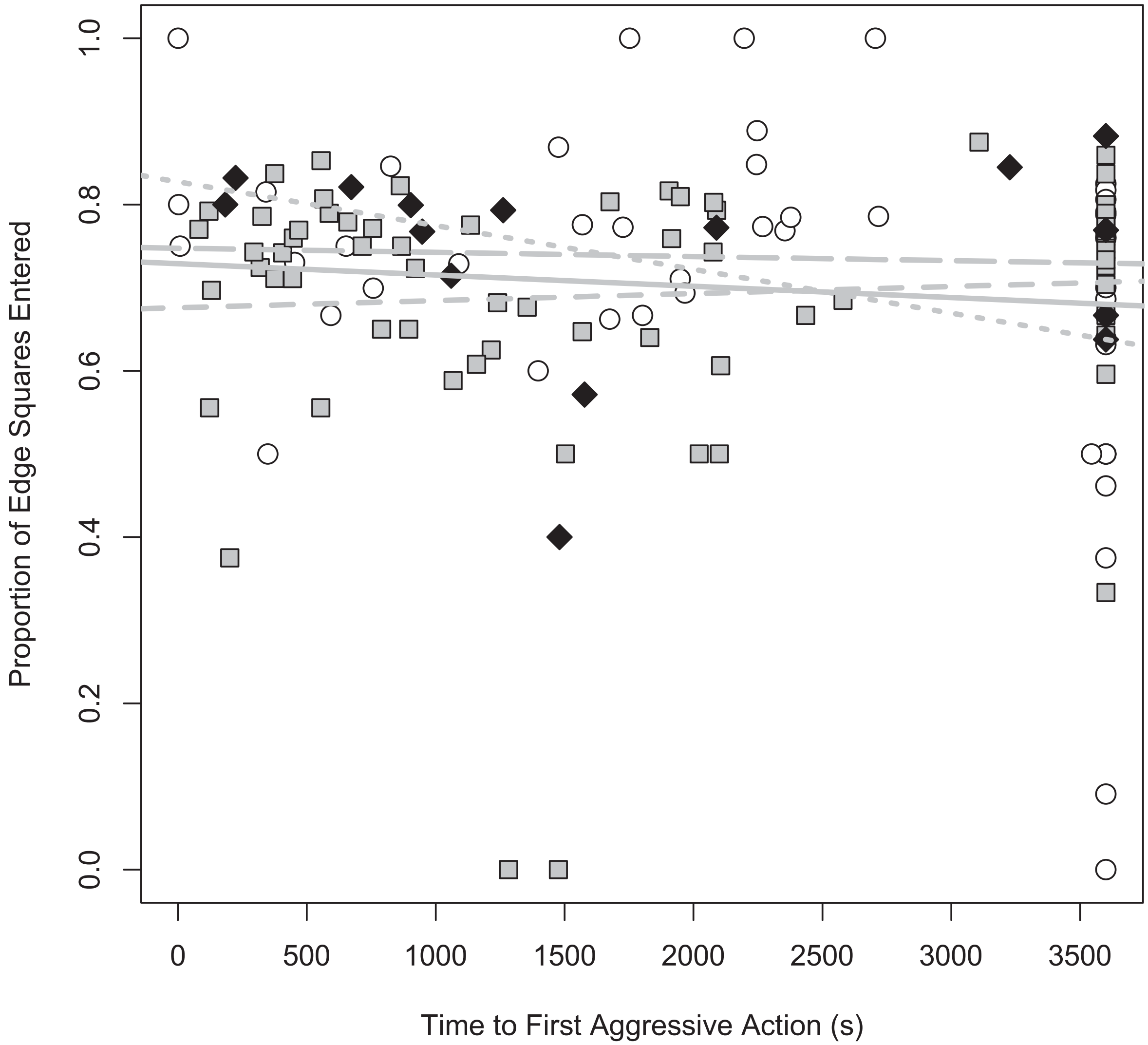

Figure S.11. The relationship between the time to first aggressive action in the mirror aggression task and the proportion of edge squares entered in the open field task. The main effect of the time to first aggressive action on the proportion of edge squares entered was found to be significant (*p* = 0.006), the interaction term with sex and color morph was also significant (*p* = 0.046). Females are indicated by white circles and dotted gray line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

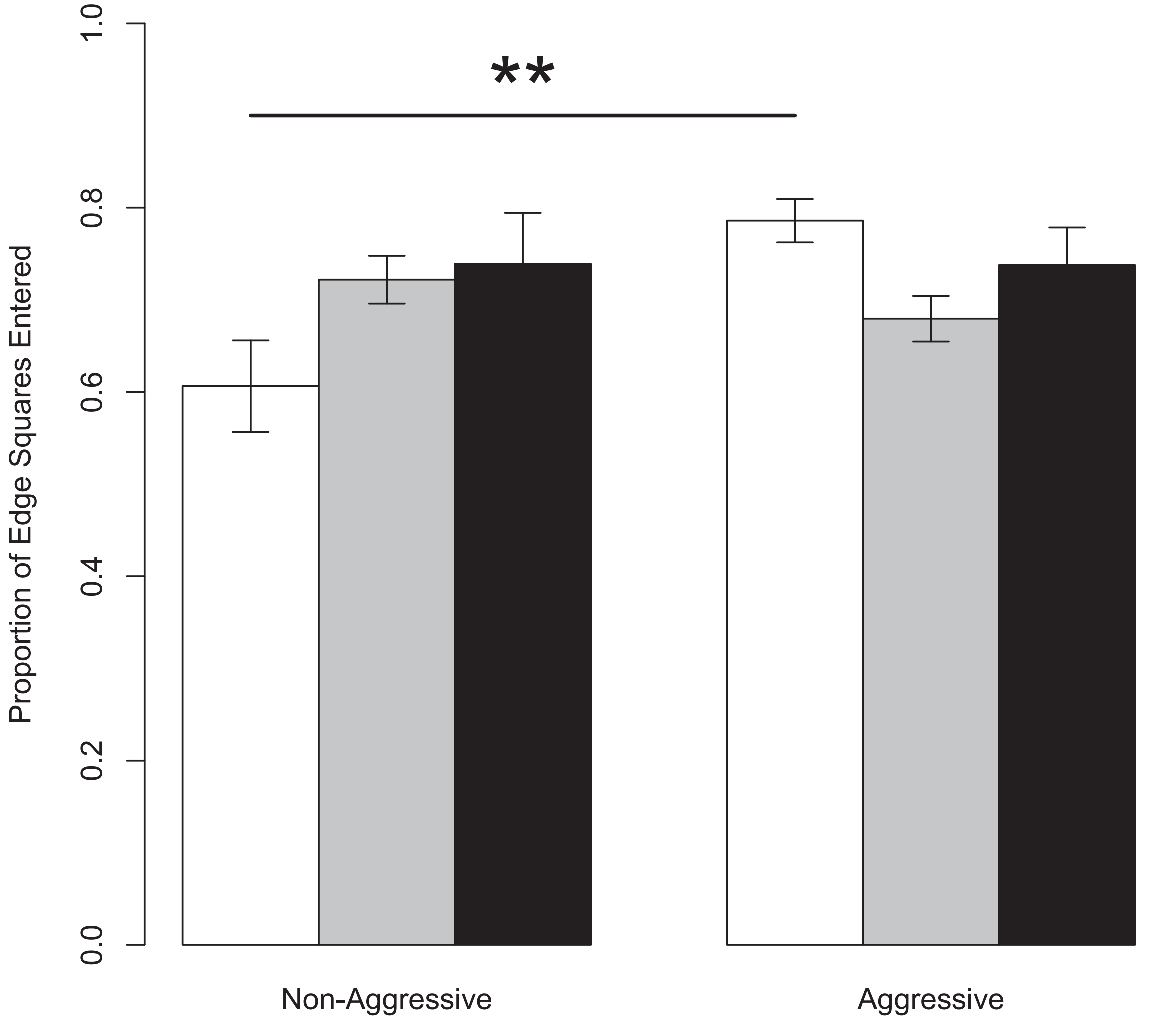

Figure S.12. Female and male color morph proportion of edge squares entered during the open field task split by whether the fish behaved aggressively or not in the mirror aggression task. Mean (± SEM) proportion of edge squares entered for females (white bar), yellow male morphs (gray bar), and red males (black bar). Both a main effect and interaction effect of color morph and aggressive/non-aggressive was seen with respect to the proportion of edge squares entered ($p < 0.001$ and $p = 0.003$ respectively). Non-aggressive and aggressive females differed significantly from each other ($p = 0.003$), but neither of the male groups differed from each other with respect to aggression.

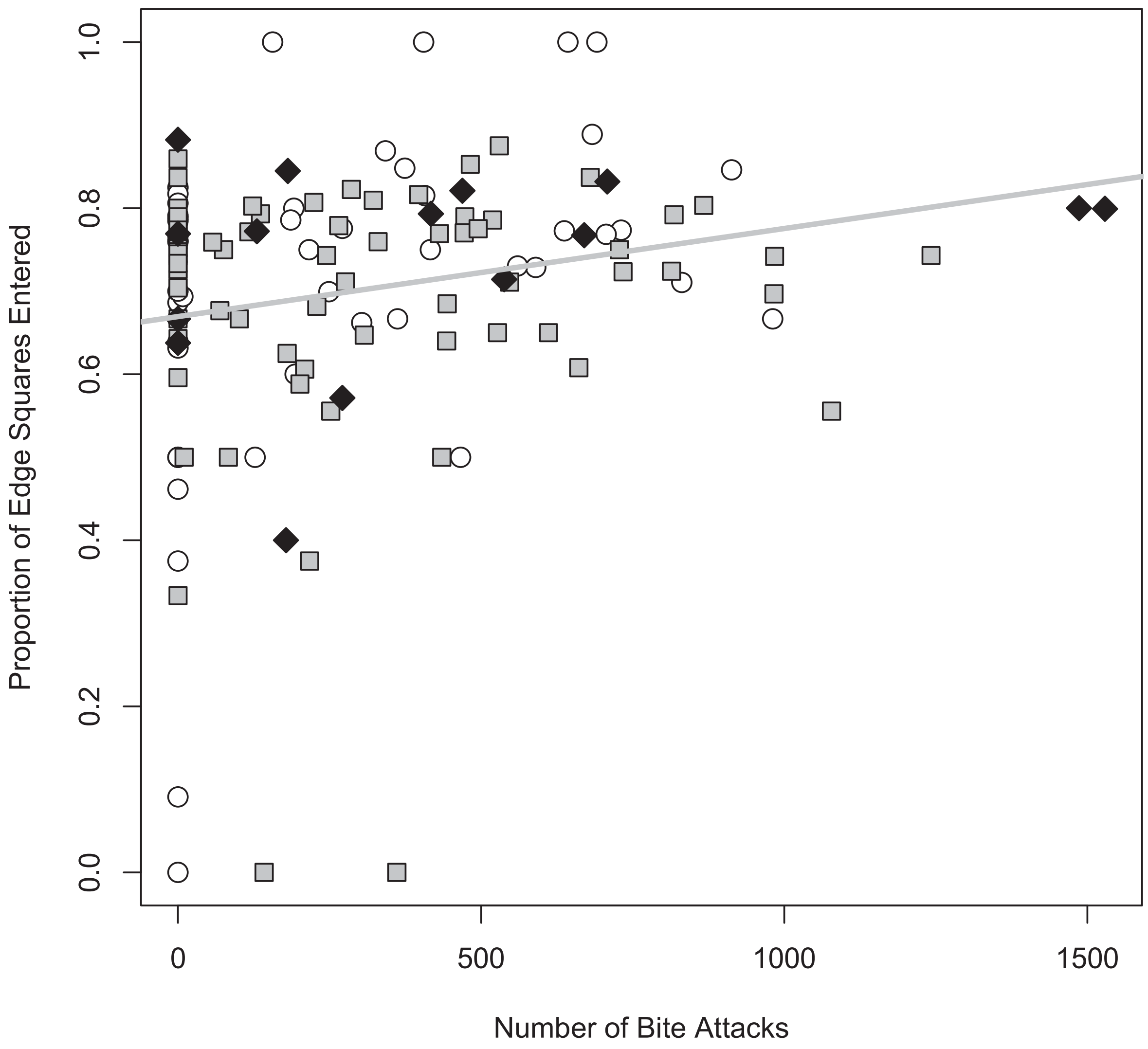

Figure S.13. The relationship between the number of bites in the mirror aggression task and the proportion of edge squares entered in the open field task. The main effect of the number of bites on the proportion of edge squares entered was found to be significant ($p = 0.003$), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; $p = 0.12$).

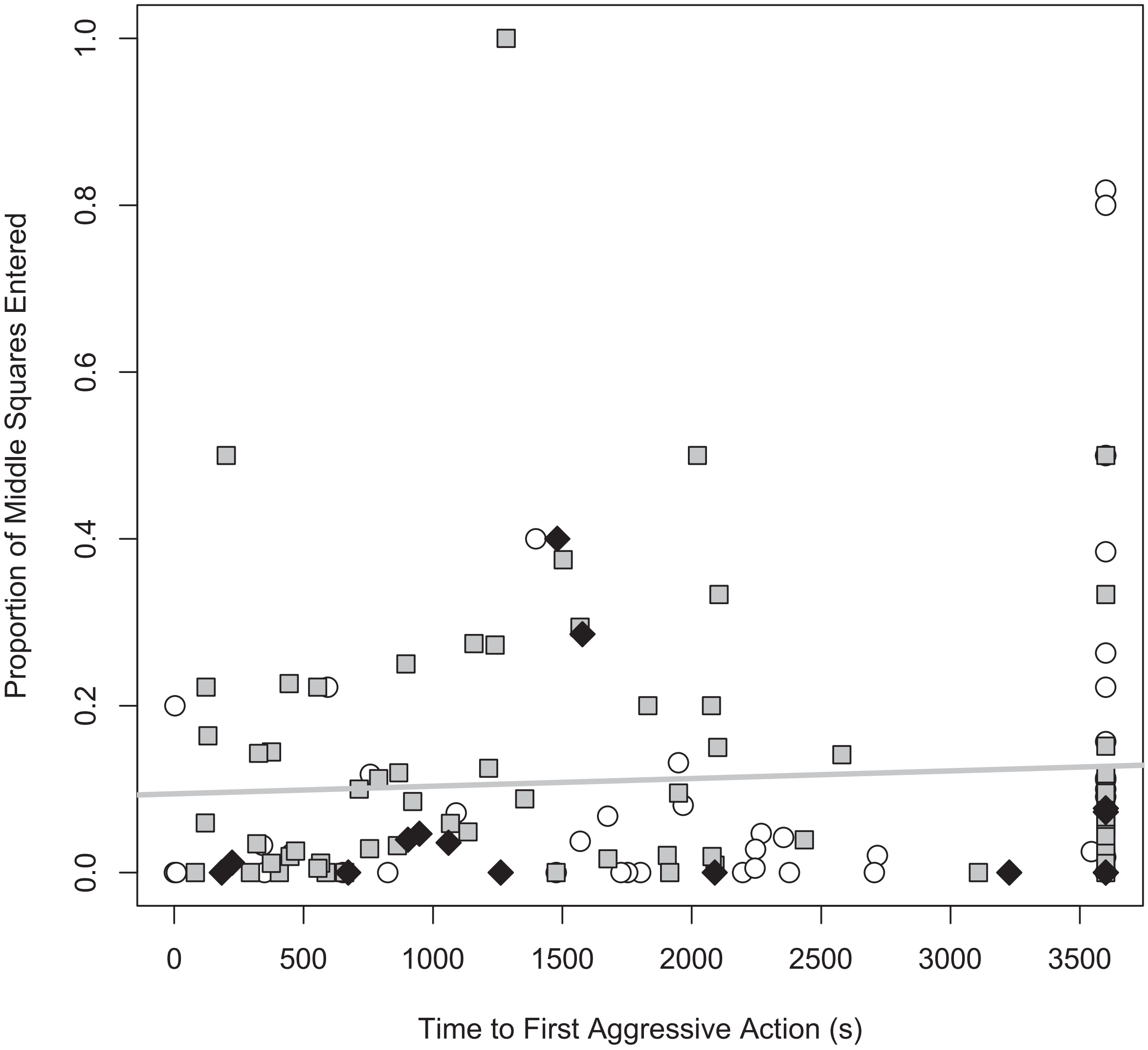

Figure S.14. The relationship between the time to first aggressive action in the mirror aggression task and the proportion of middle squares entered during the open field task. The main effect of the time to first aggressive action on the proportion of middle squares entered was significant (*p* = 0.04), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; *p* = 0.15).

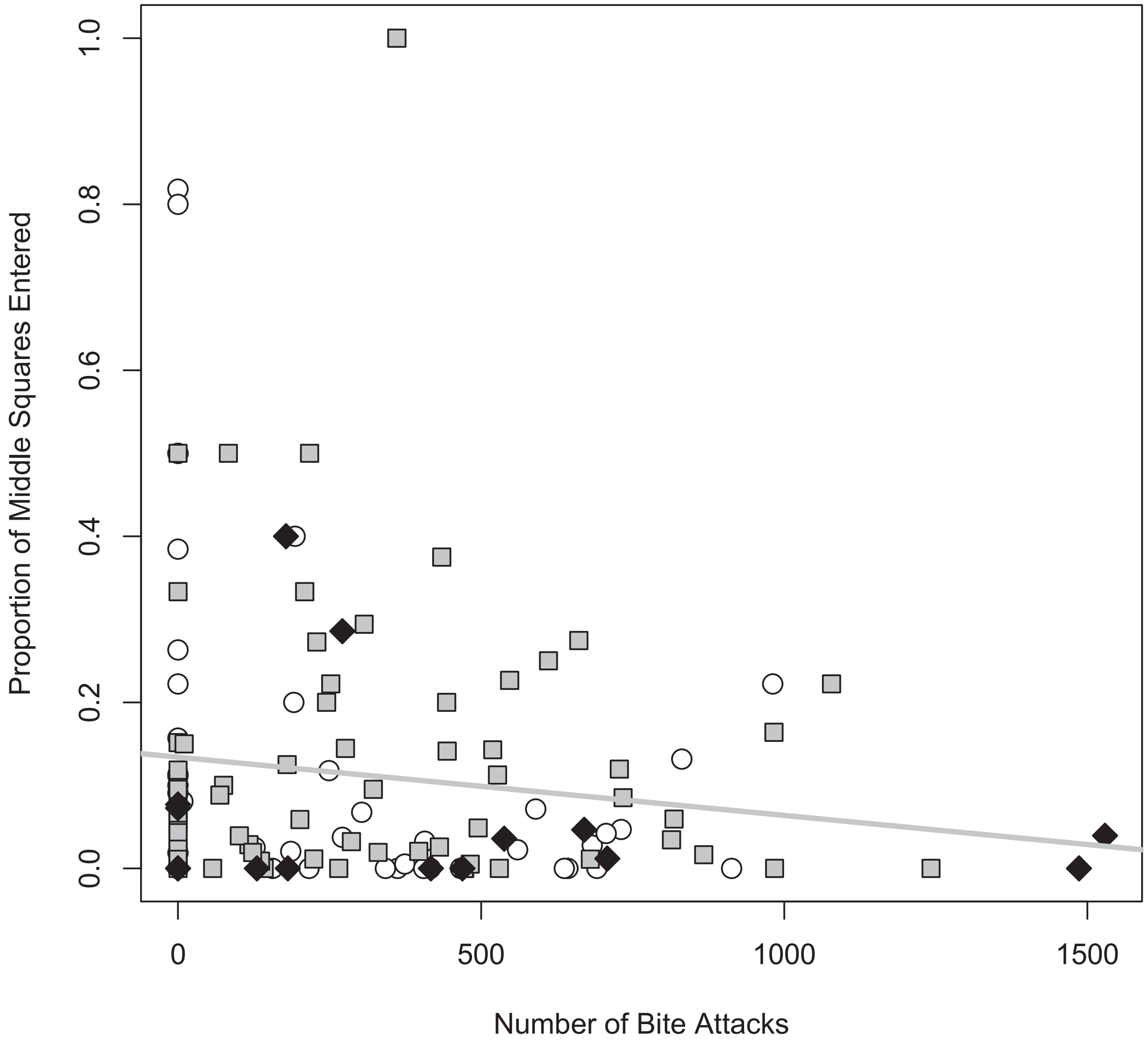

Figure S.15. The relationship between the number of bites from the mirror aggression task and the proportion of middle squares entered during the open field task. The main effect of the number of bites on the proportion of middle squares entered was significant (*p* = 0.03), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; *p* = 0.27).

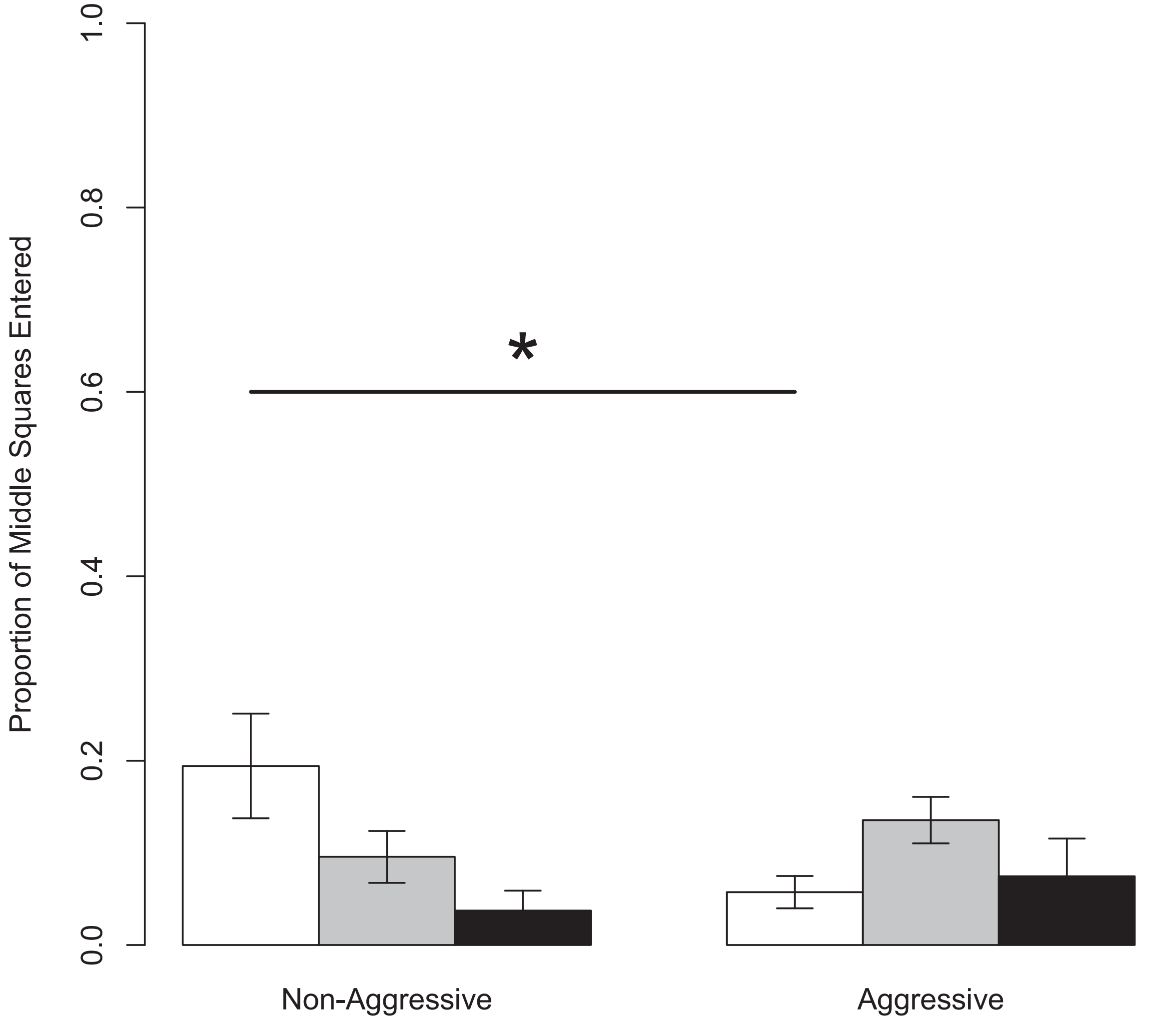

Figure S.16. Female and male color morph proportion of middle squares entered during the open field task split by whether the fish behaved aggressively or not in the mirror aggression task. Mean (± SEM) proportion of middle squares entered for females (white bar), yellow male morphs (gray bar), and red males (black bar). Both a main effect and interaction effect of color morph and aggressive/non-aggressive was seen with respect to the proportion of middle squares entered (*p* = 0.006 and *p* = 0.03 respectively). Non-aggressive and aggressive females differed significantly from each other (*p* = 0.03), but neither of the male groups differed from each other with respect to aggression.

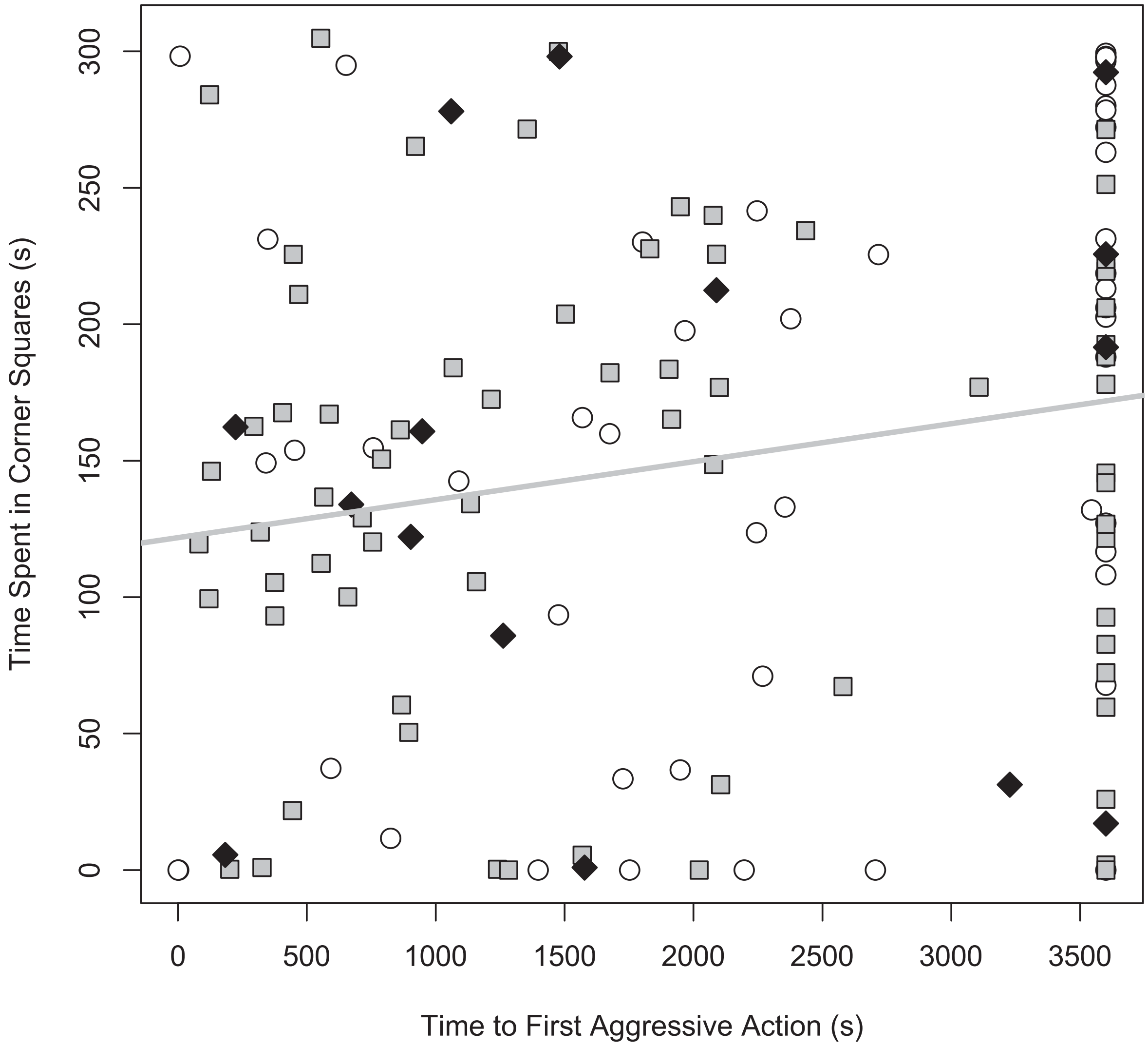

Figure S.17. The relationship between the time to first aggressive action in the mirror aggression task and the time spent in corner squares during the open field task. The main effect of the time to first aggressive action on the time spent in corner squares was significant (*p* = 0.004), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; *p* = 0.11)

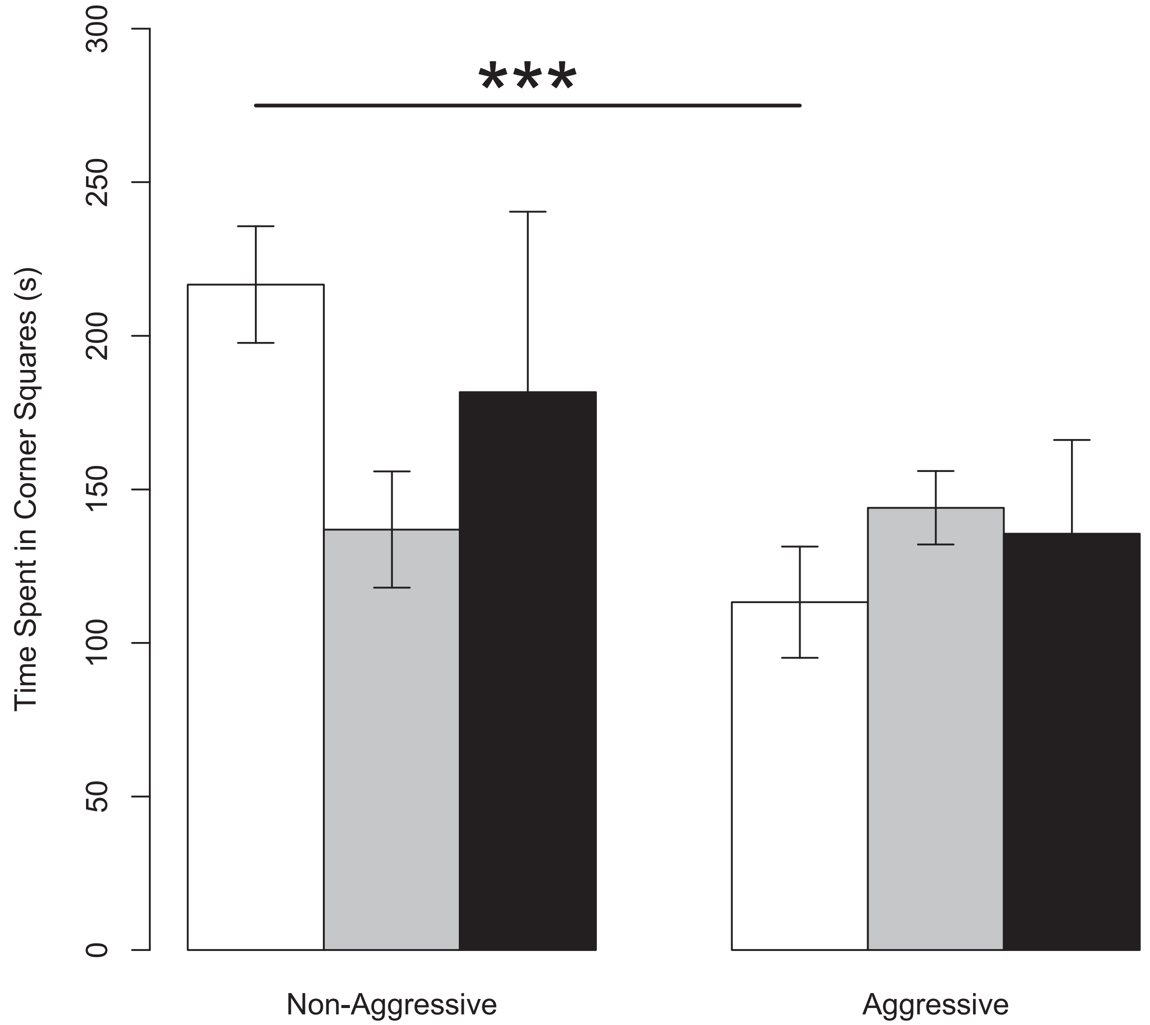

Figure S.18. Female and male color morph time spent in corner squares during the open field task split by whether the fish behaved aggressively or not in the mirror aggression task. Mean (± SEM) time spent in corner squares for females (white bar), yellow male morphs (gray bar), and red males (black bar). Both a main effect and interaction effect of color morph and aggressive/non-aggressive was seen with respect to the proportion of middle squares entered ($p < 0.001$ and $p = 0.009$ respectively). Non-aggressive and aggressive females differed significantly from each other ($p < 0.001$), but neither of the male groups differed from each other with respect to aggression.

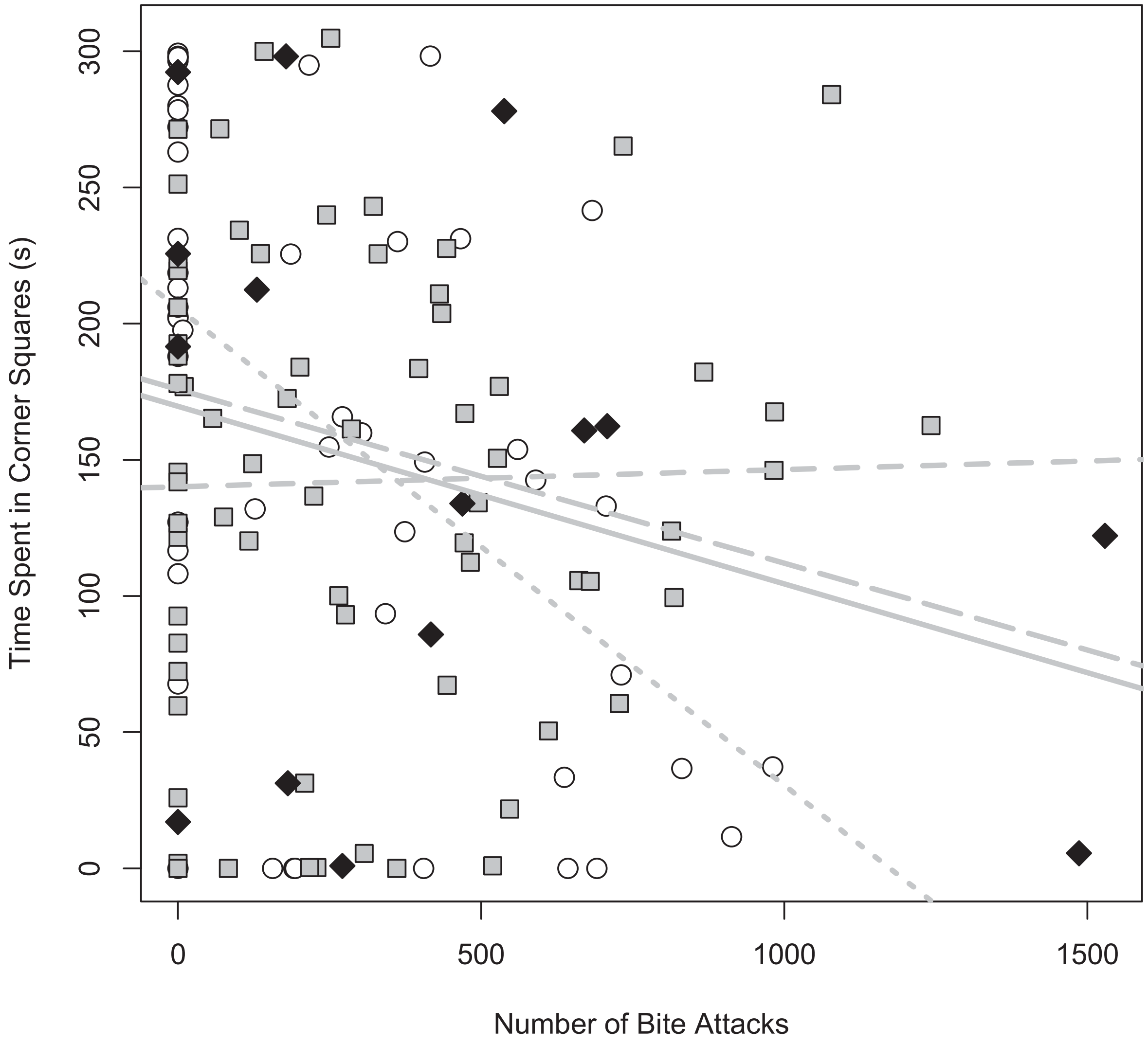

Figure S.19. The relationship between the number of bites in the mirror aggression task and the time spent in corner squares during the open field task. The main effect of the number of bites on the time spent in corner squares was significant (solid line, $p < 0.001$), as was the interaction term with sex and color morph ($p = 0.01$). Females are indicated by white circles and dotted gray line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

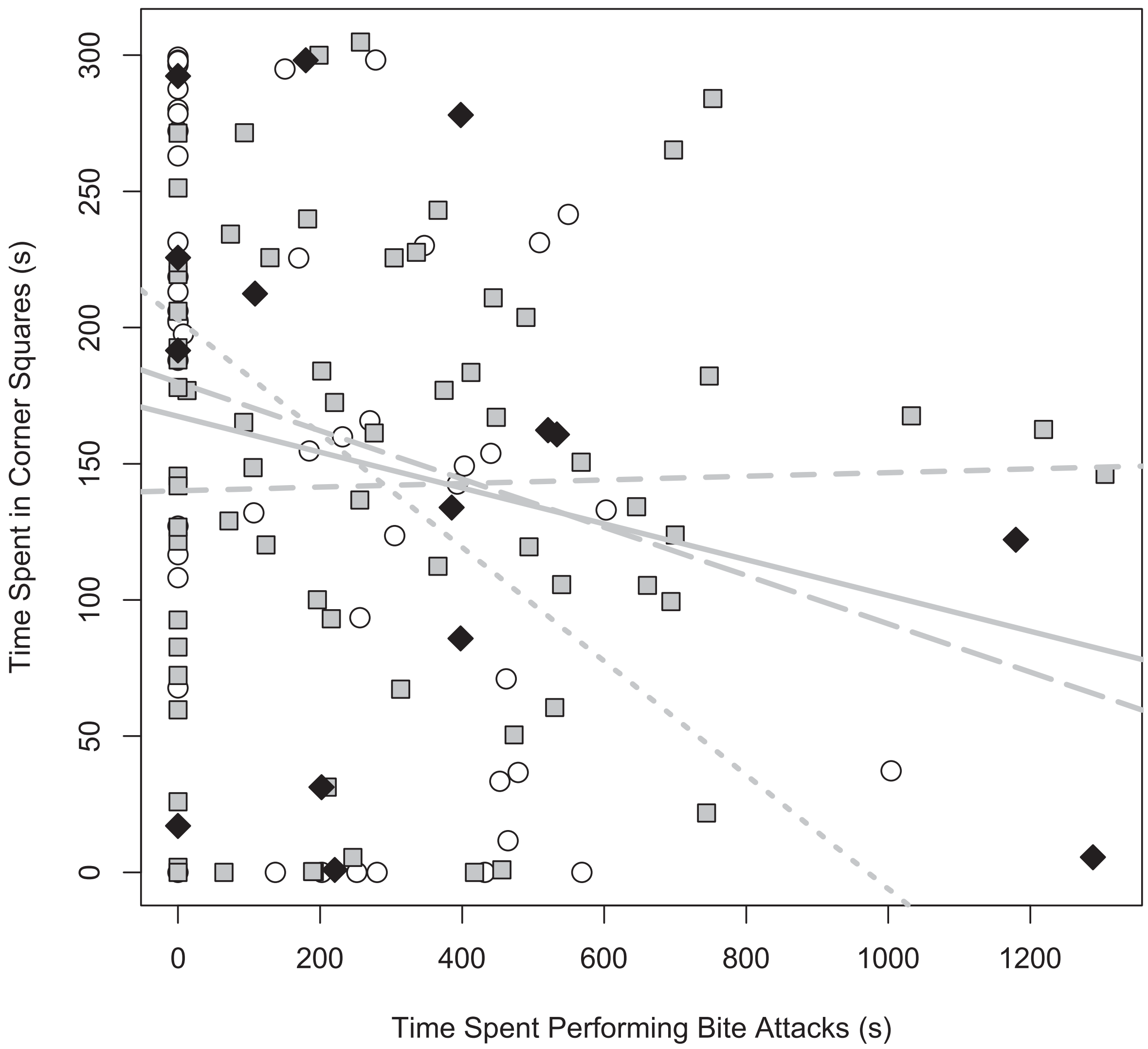

Figure S.20. The relationship between the time spent performing bites in the mirror aggression task and the time spent in corner squares during the open field task. The main effect of the time spent performing bites on the time spent in corner squares was significant (solid line, $p < 0.001$), as was the interaction term with sex and color morph ($p = 0.005$). Females are indicated by white circles and dotted line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

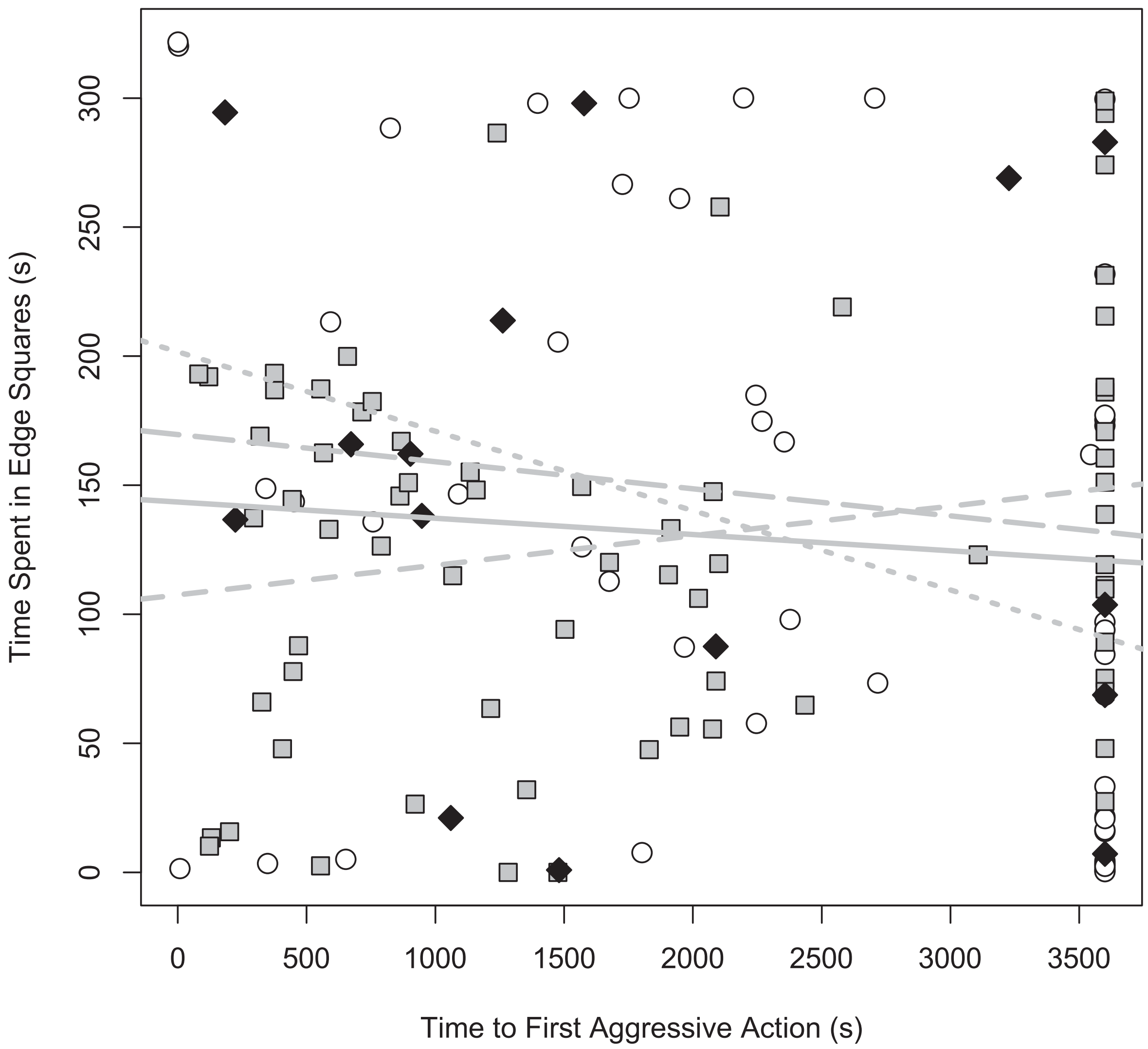

Figure S.21. The relationship between the time to first aggressive action in the mirror aggression task and the time spent in edge squares during the open field task. The main effect of the time to first aggressive action on the time spent in edge squares was significant (solid line, *p* = 0.002), as was the interaction term with sex and color morph (*p* = 0.01). Females are indicated by white circles and dotted line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

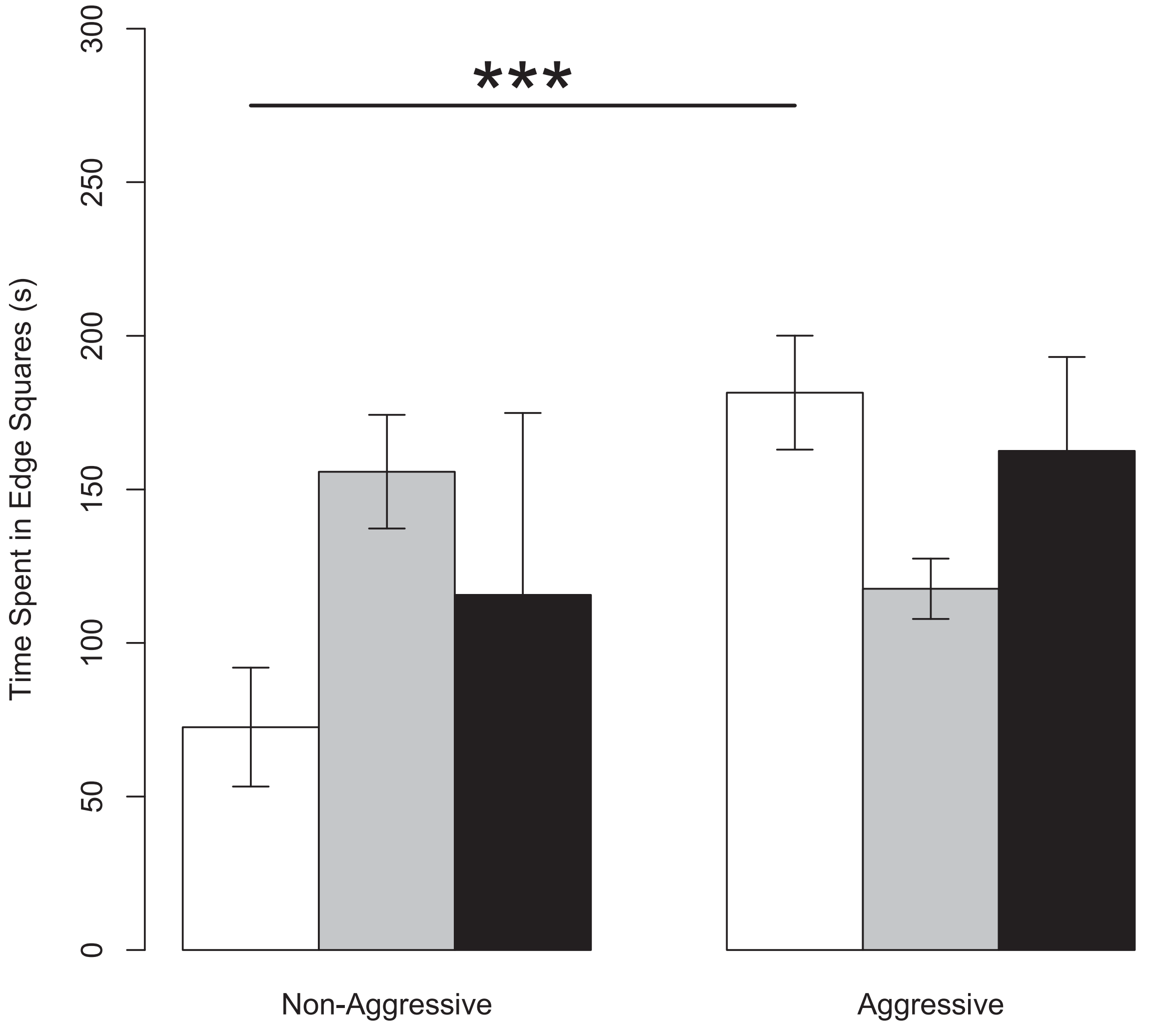

Figure S.22. Female and male color morph time spent in edge squares during the open field task split by whether the fish behaved aggressively or not in the mirror aggression task. Mean (± SEM) time spent in edge squares for females (white bar), yellow male morphs (gray bar), and red males (black bar). Both a main effect and interaction effect of color morph and aggressive/non-aggressive was seen with respect to the proportion of middle squares entered ($p < 0.001$ for both). Non-aggressive and aggressive females differed significantly from each other ($p < 0.001$), but neither of the male groups differed from each other with respect to aggression.

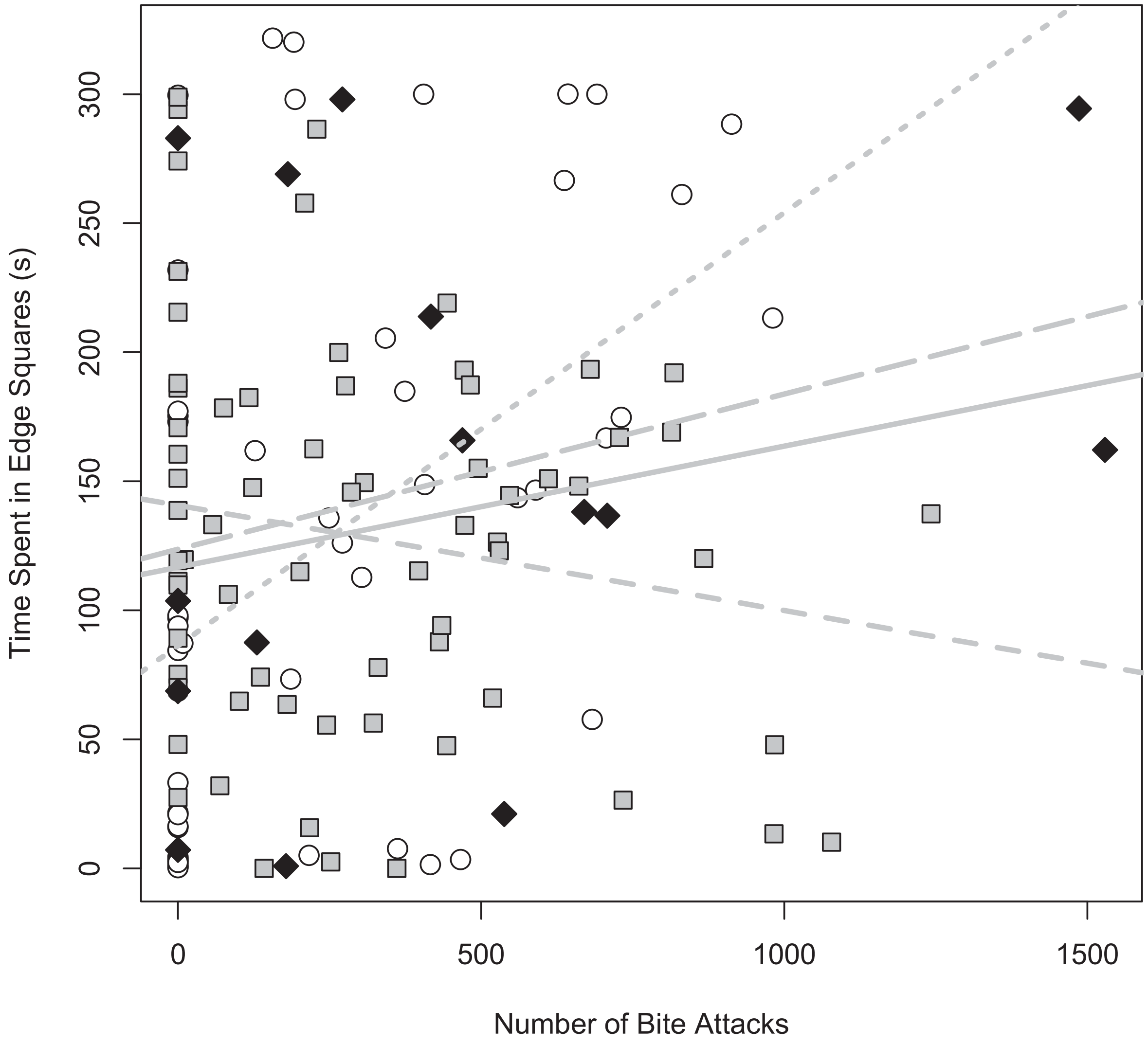

Figure S.23. The relationship between the number of bites in the mirror aggression task and the time spent in edge squares during the open field task. The main effect of the number of bites on the time spent in edge squares was significant (solid line, $p < 0.001$), as was the interaction term with sex and color morph ($p < 0.001$). Females are indicated by white circles and dotted line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

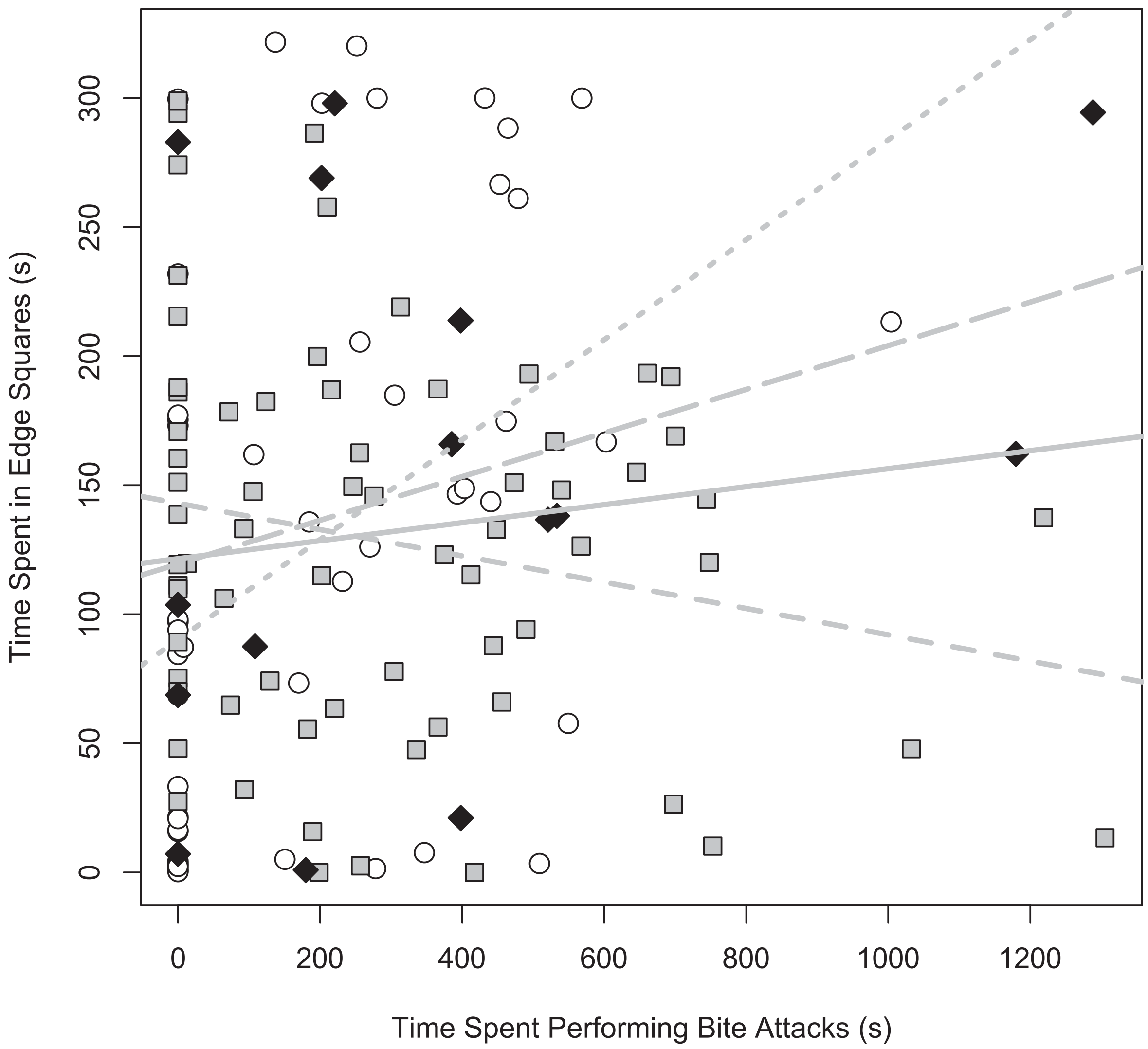

Figure S.24. The relationship between the time spent performing bites in the mirror aggression task and the time spent in edge squares during the open field task. The main effect of the time spent performing bites on the time spent in edge squares was significant (solid line, $p < 0.001$), as was the interaction term with sex and color morph ($p < 0.001$). Females are indicated by white circles and dotted line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

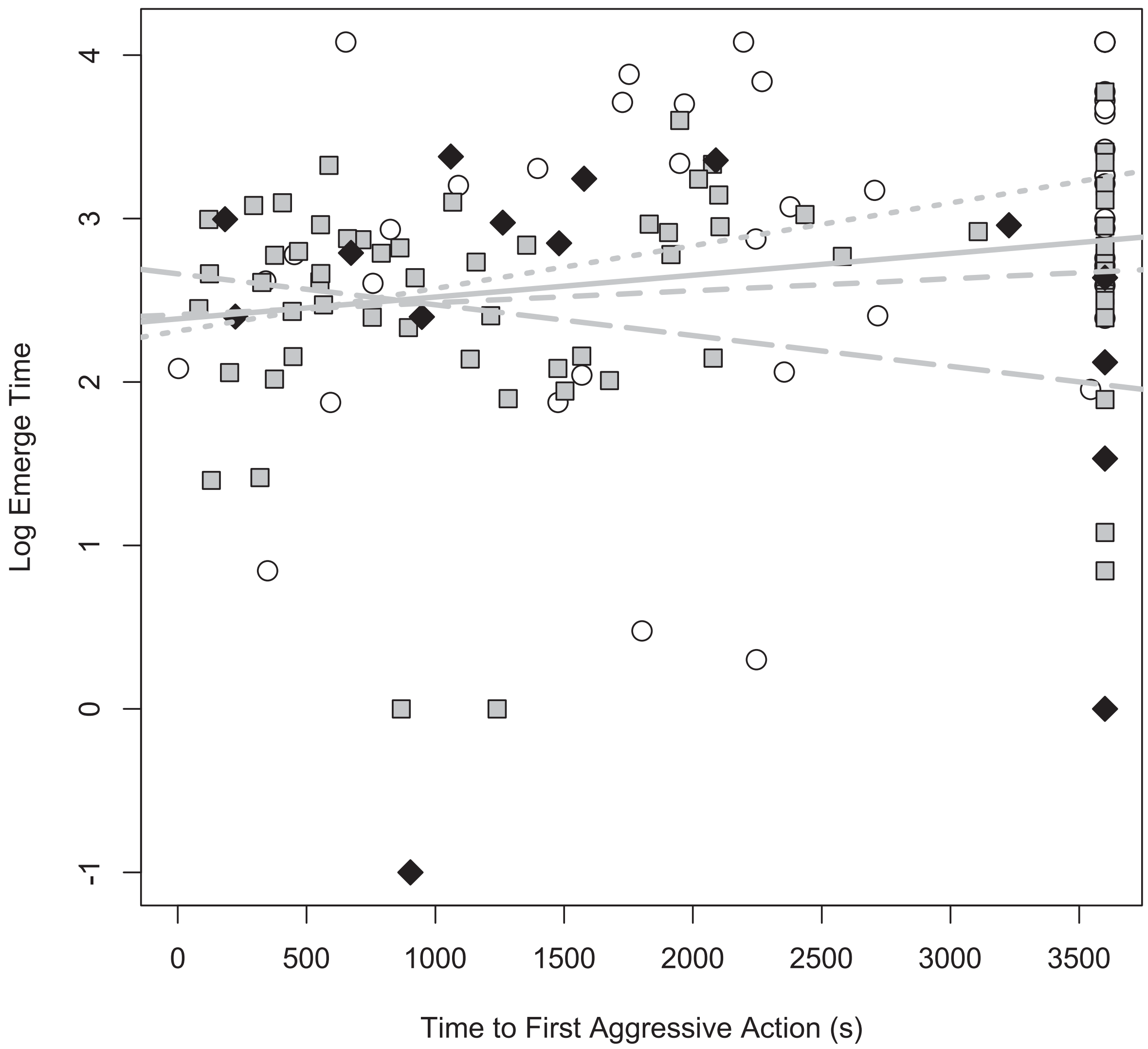

Figure S.25. The relationship between the time to first aggressive action in the mirror aggression task and the log transformed time to emerge from the novel environment emergence task. The main effect of the number of bites on the time spent in corner squares was significant (solid line, *p* = 0.01) and the interaction term with sex and color morph trended towards significance (*p* = 0.07). Females are indicated by white circles and dotted line, the gray boxes and the short dashed line indicate yellow males and the interaction effect, and red males are indicated by the black diamonds and long dashed line.

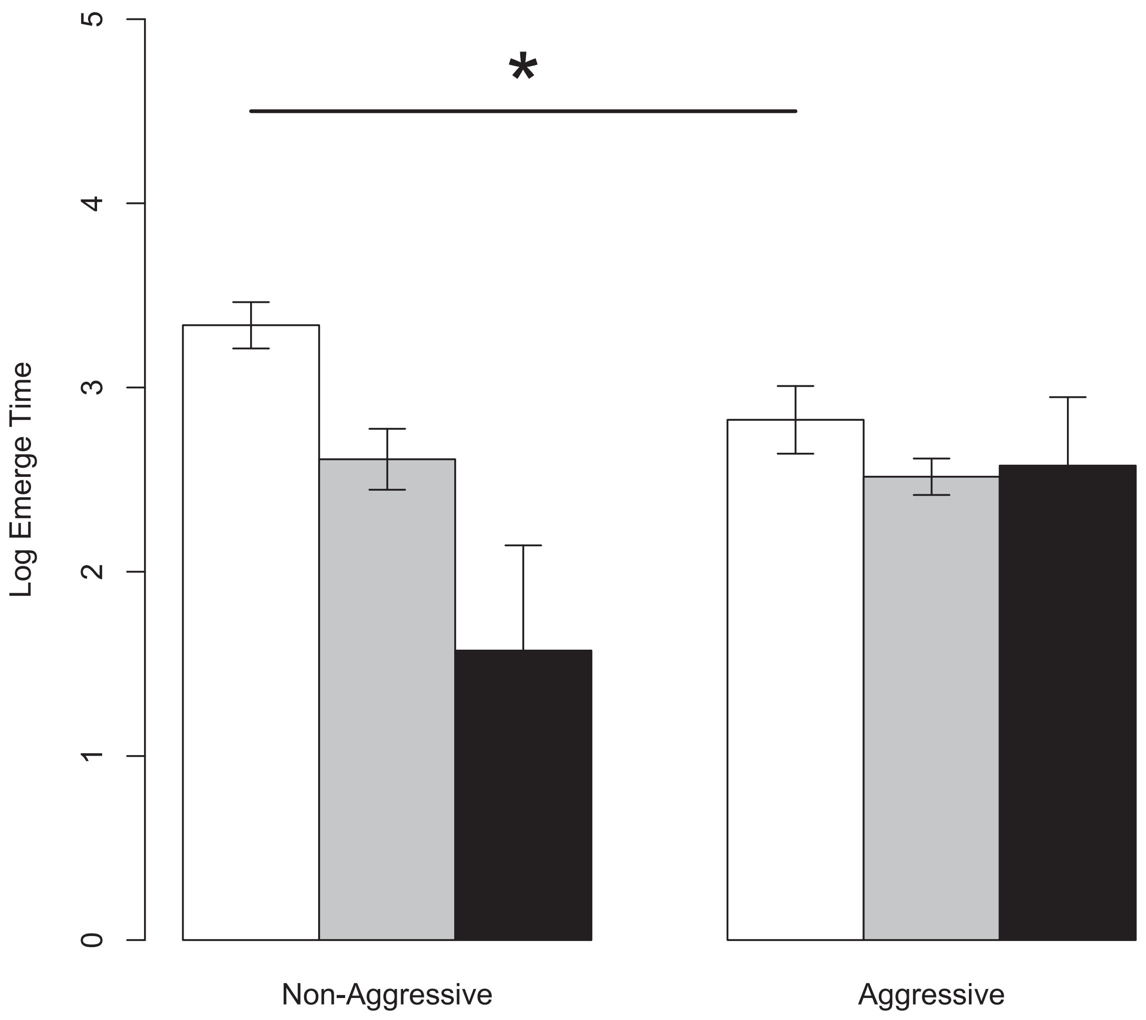

Figure S.26. Female and male color morph log emerge times in the novel environment emergence task split by whether the fish behaved aggressively or not in the mirror aggression task. Mean (± SEM) times to emerge action for females (white bar), yellow male morphs (gray bar), and red males (black bar). Both a main effect and interaction effect of color morph and aggressive/non-aggressive was seen with respect to the log emerge time (p = 0.03 and p = 0.02 respectively). Non-aggressive and aggressive females differed significantly from each other (p = 0.03), but neither of the male groups differed from each other with respect to aggression.

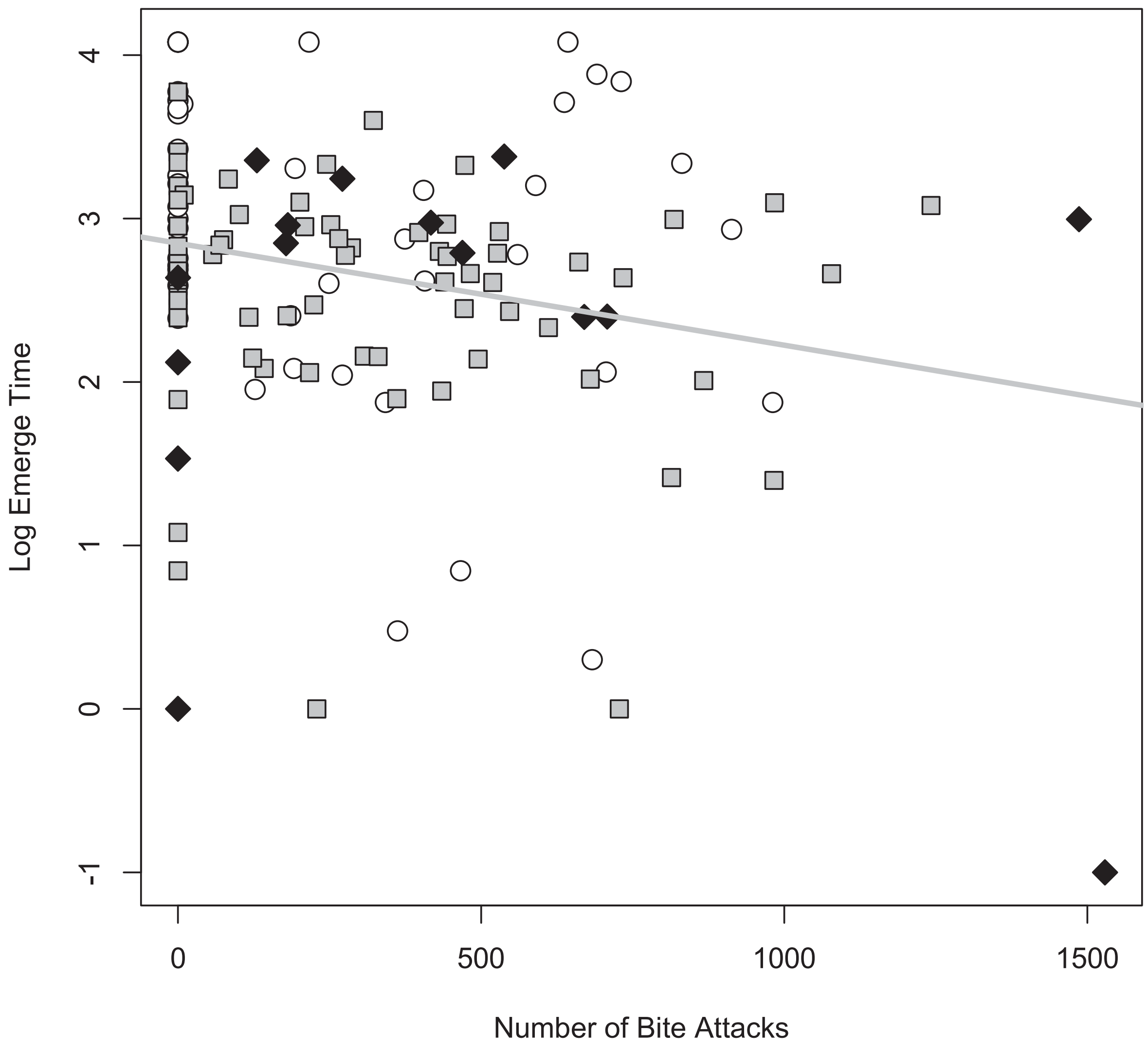

Figure S.27. The relationship between the number of bites in the mirror aggression task and the log transformed time to emerge from the novel environment emergence task. The main effect of the number of bites on the log emerge time was significant ($p = 0.048$), while the interaction term with sex and color morph was not (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; $p = 0.63$).

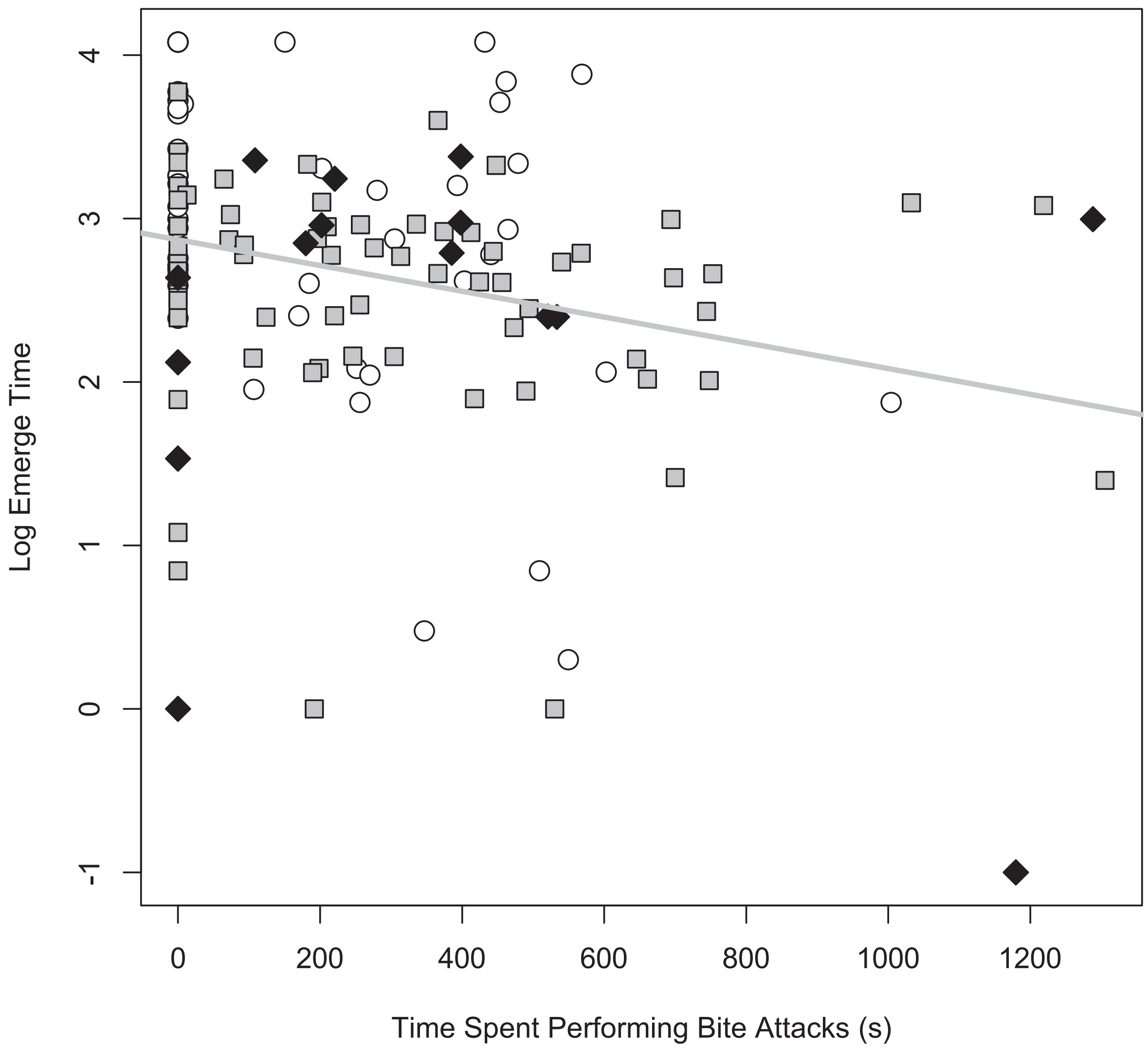

Figure S.28. The relationship between the time spent performing bites in the mirror aggression task and the log transformed time to emerge from the novel environment emergence task. The main effect of the time spent performing bites on the log emerge time was significant (*p* = 0.004), while the interaction term with sex and color morph was not (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; *p* = 0.16).

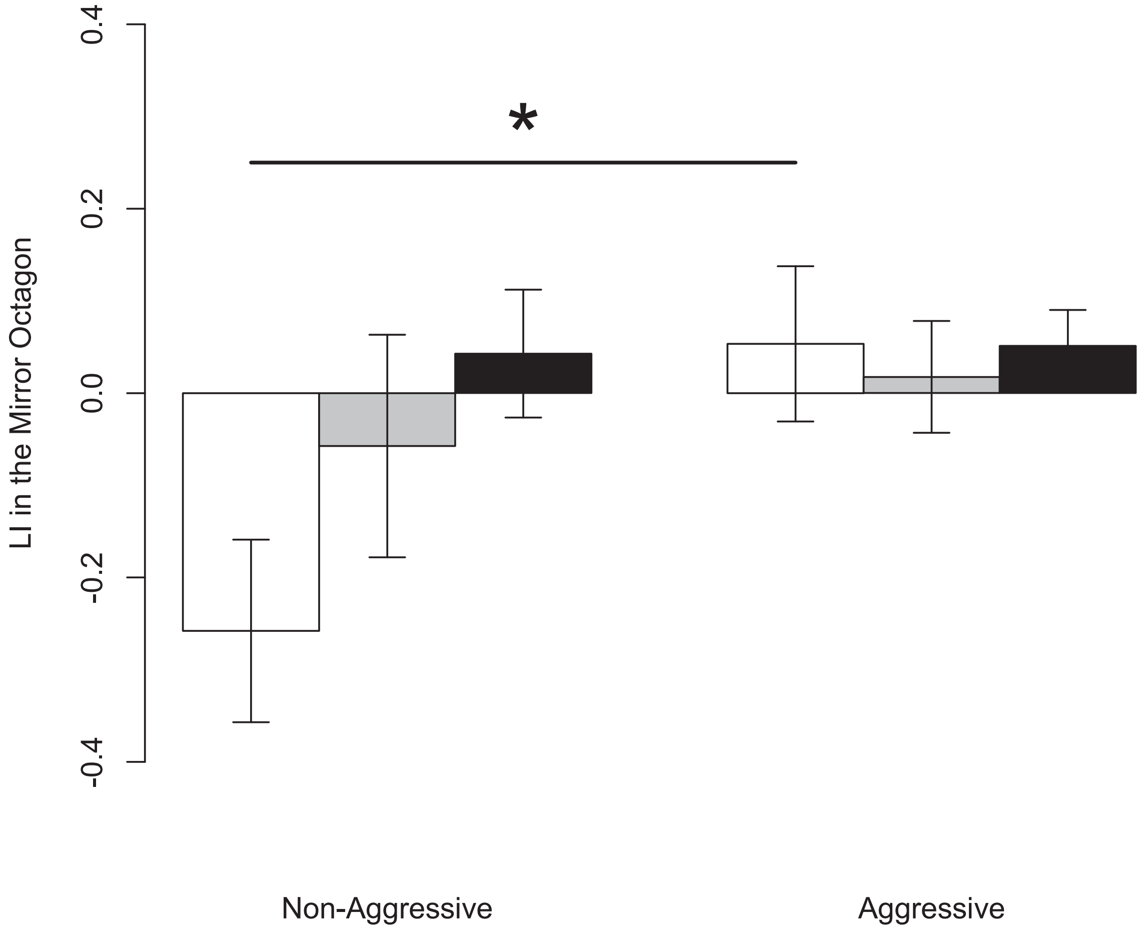

Figure S.29. The relationship between whether the fish behaved aggressively or not in the mirror aggression task and the lateralization index (LI) from the mirror octagon. Mean (± SEM) LI based on whether the fish was aggressive or non-aggressive (*p* = 0.01). There was no effect of the interaction of aggressive/not aggressive and sex and color morph on the LI (*p* = 0.31). Although non-aggressive and aggressive females differed significantly from each other (*p* = 0.02), but neither of the male groups differed from each other with respect to aggression.

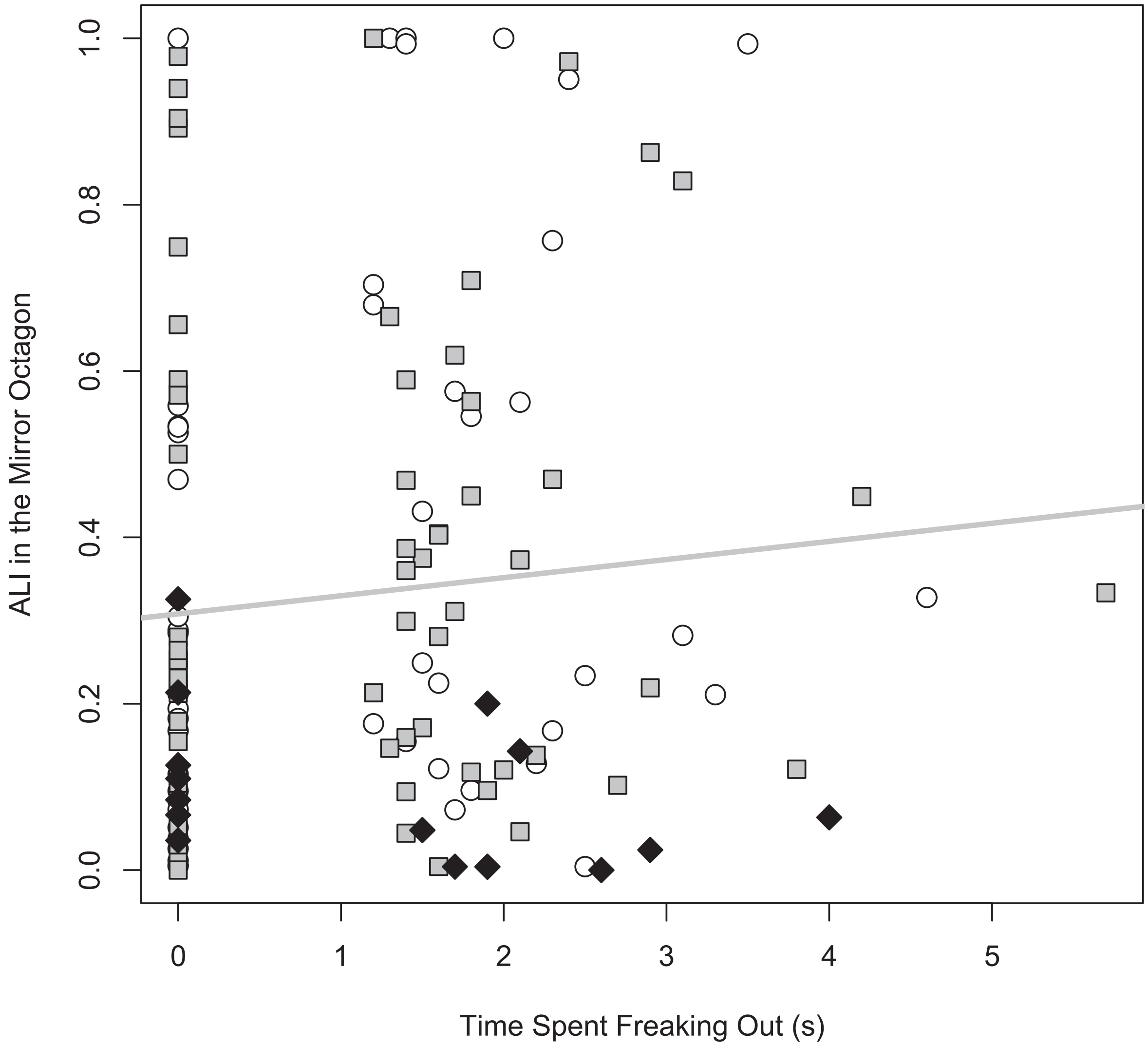

Figure S.30. The relationship between the time spent “freaking-out” in the open field task and the absolute lateralization index (ALI) from the mirror octagon task. The main effect of time spent “freaking-out” was significant with respect to the ALI in the mirror octagon ($p = 0.05$), the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; $p = 0.26$).

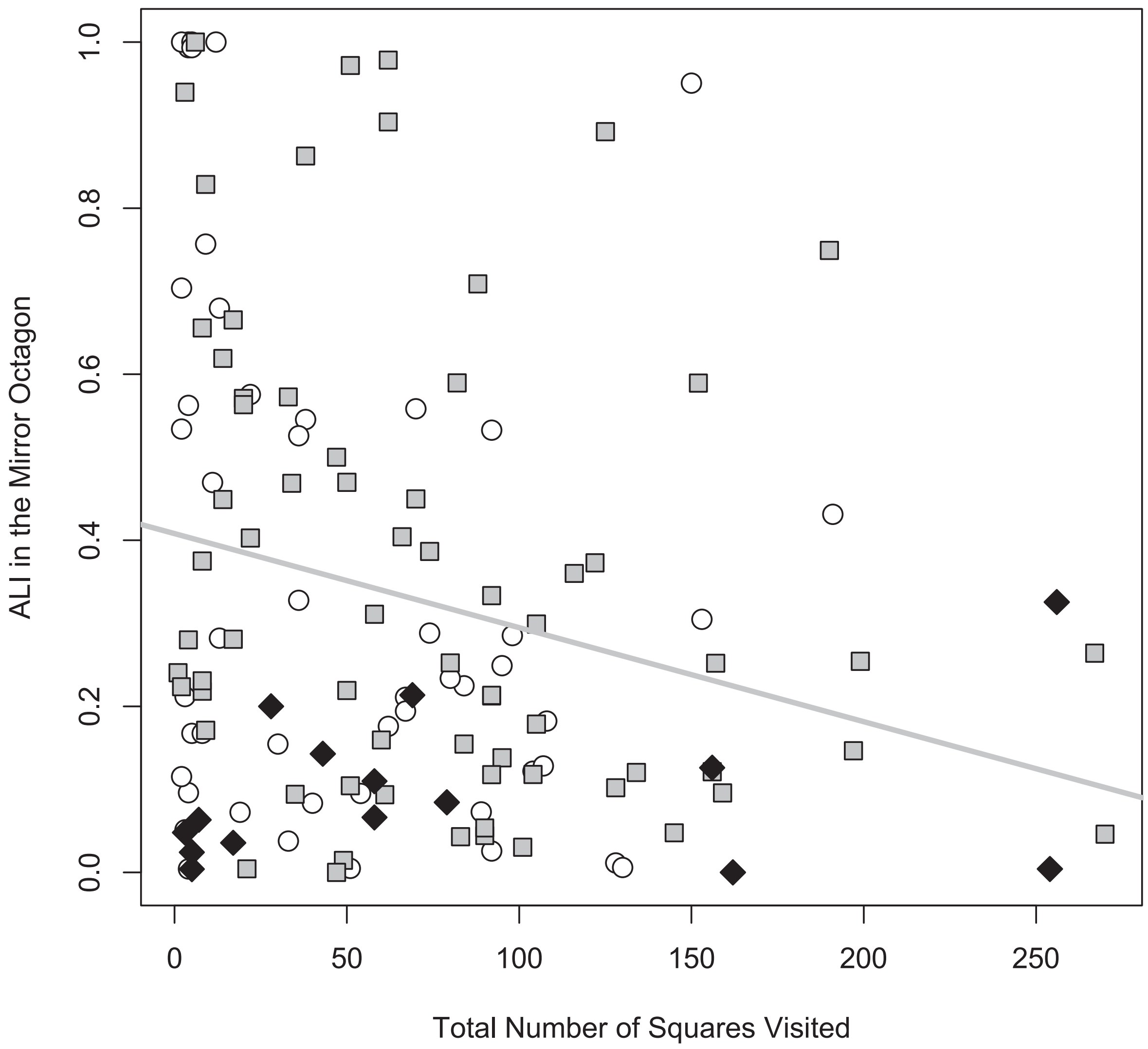

Figure S.31. The relationship between the total number of squares entered and the absolute lateralization index (ALI) from the mirror octagon task. The main effect of the total squares entered on ALI in the mirror octagon was found to be significant (solid line, *p* = 0.03), while the interaction term with sex and color was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; *p* = 0.17).

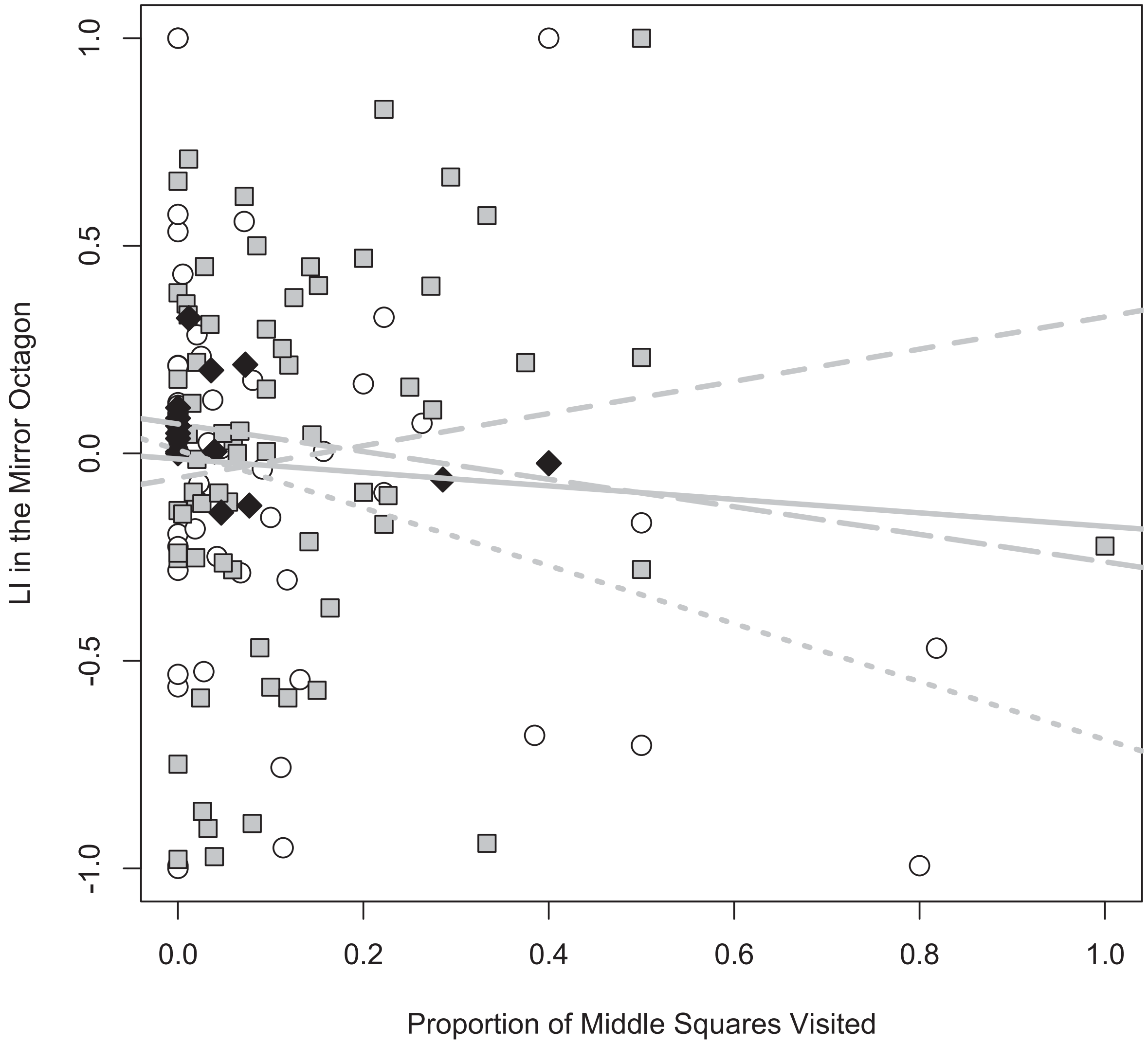

Figure S.32. The relationship between the proportion of middle squares entered and the lateralization index (LI) from the mirror octagon task. The main effect of the proportion of middle squares entered on LI in the mirror octagon was found to be significant (solid line, *p* = 0.03), while the interaction term with sex and color morph trended towards significance (females shown as white circles and dotted line, yellow males shown as gray squares and short dashed line, and red males shown as black diamonds and long dashed line; *p* = 0.06).

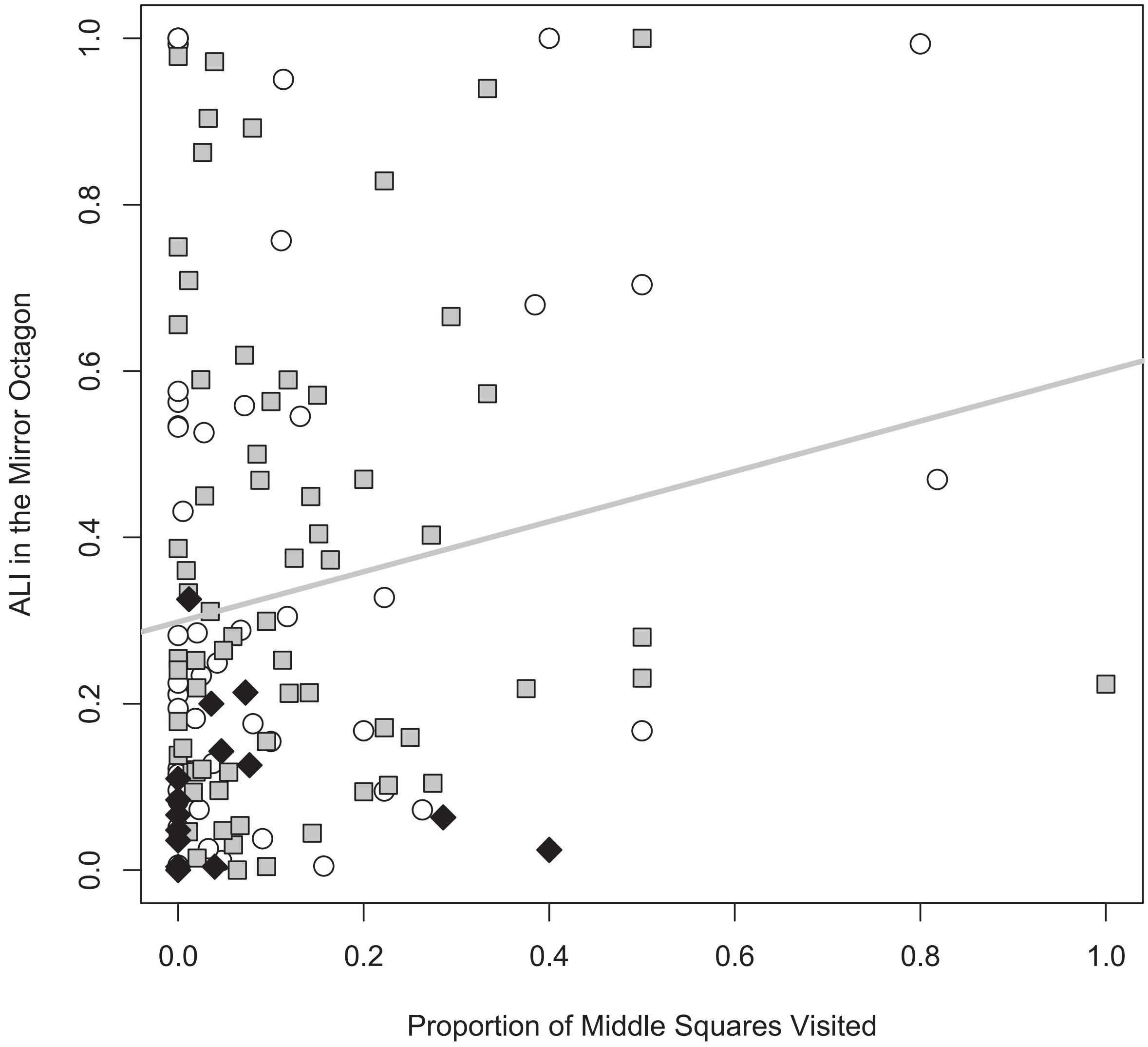

Figure S.33. The relationship between the proportion of middle squares entered and the absolute lateralization index (ALI) from the mirror octagon task. The main effect of the proportion of middle squares entered on ALI in the mirror octagon was found to be significant ($p = 0.04$), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; $p = 0.47$).

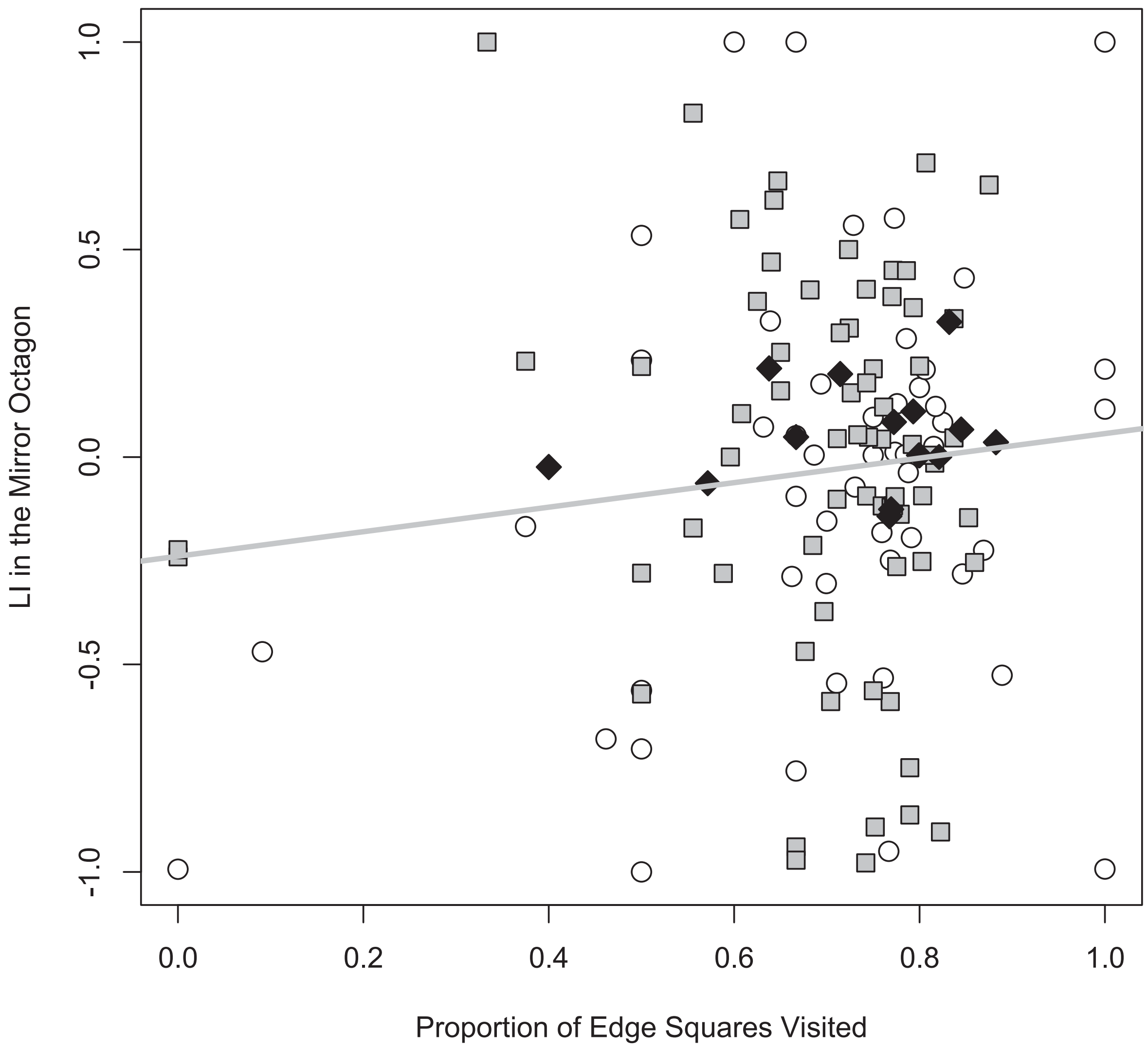

Figure S.34. The relationship between the proportion of edge squares entered and the lateralization index (LI) from the mirror octagon task. The main effect of the proportion of edge squares entered on LI in the mirror octagon was found to be significant ($p = 0.02$), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; $p = 0.14$).

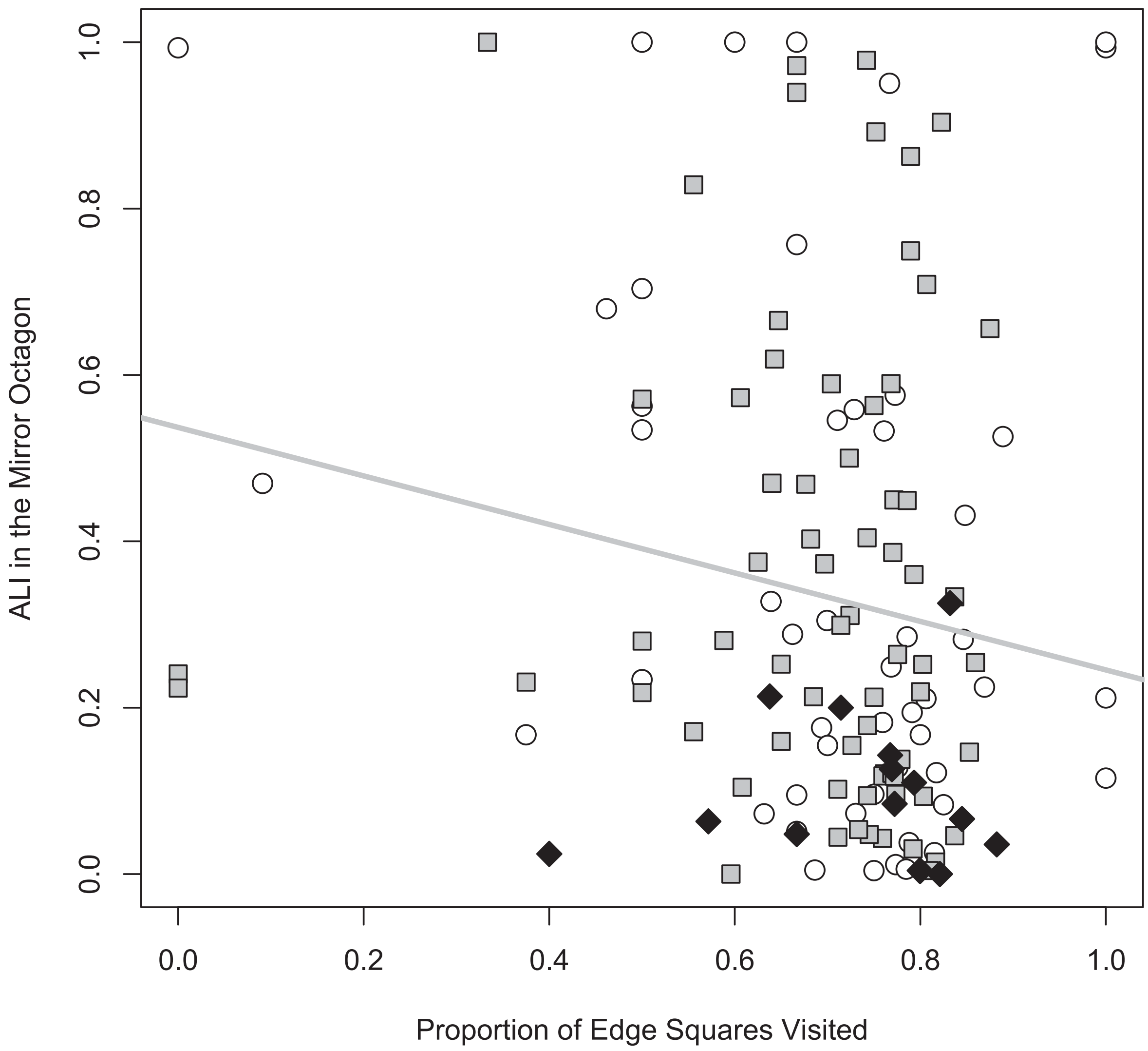

Figure S.35. The relationship between the proportion of edge squares entered and the absolute lateralization index (ALI) from the mirror octagon task. The main effect of the proportion of edge squares entered on ALI in the mirror octagon was found to be significant ($p = 0.04$), while the interaction term with sex and color morph was not significant (females shown as white circles, yellow males shown as gray squares, and red males shown as black diamonds; $p = 0.48$).

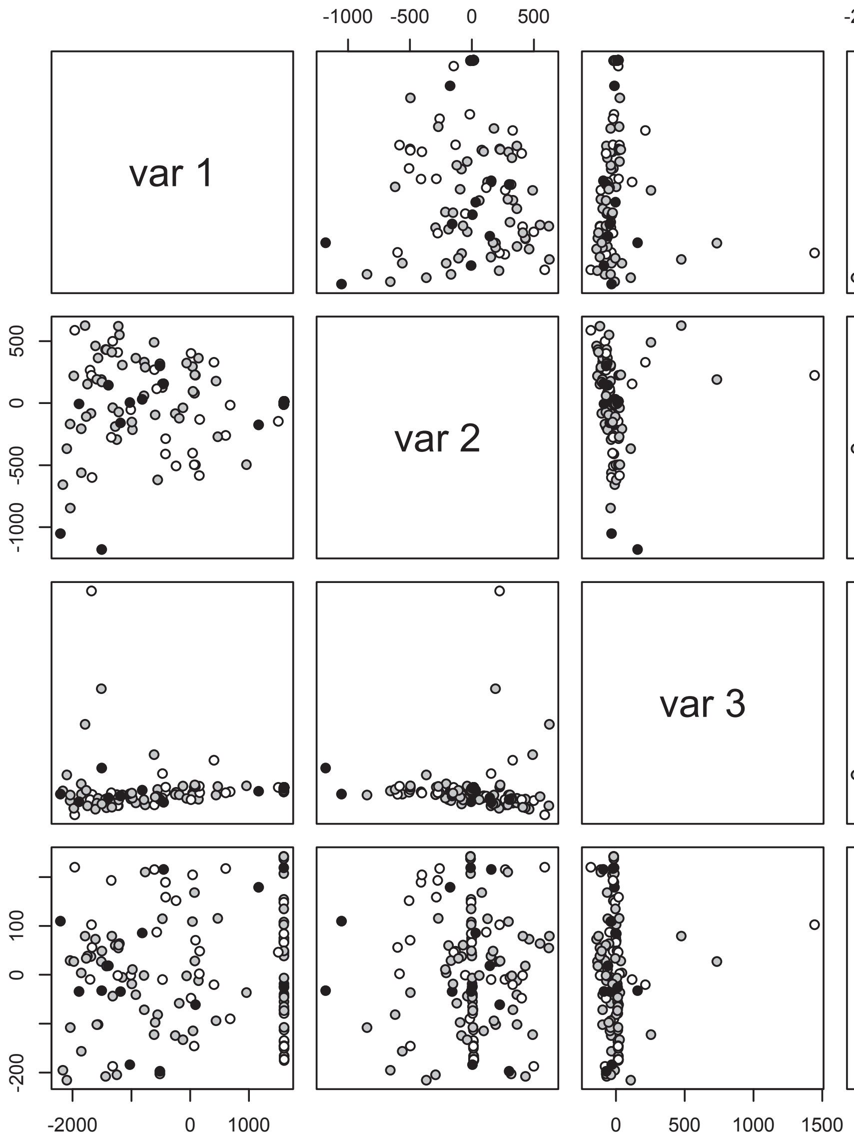

Figure S.36. Multidimensional scaling plot.

Complete References

Adams, C.F., Liley, N.R., & Gorzalka, B. B. (1996). PCPA increases aggression in male firemouth cichlids. *Pharmacology,* 53(5), 328-330. doi: 10.1159/000139446

Ariyomo, T. O., & Watt, P. J. (2013). Aggression and sex differences in lateralization in the zebrafish. *Animal Behaviour*, *86*(3), 617–622. doi:10.1016/j.anbehav.2013.06.019

Arnott, G., Ashton, C., & Elwood, R. W. (2011). Lateralization of lateral displays in convict cichlids. *Biology Letters*, *7*(5), 683–5. doi:10.1098/rsbl.2011.0328

Axelrod, H. R. (1996). *The most complete colored lexicon of cichlids* (2nd ed.). Neptune City, T.F.H. Publications, Inc.

Bakker, T. (1985). Two-way selection for aggression in juvenile, female and male sticklebacks (Gasterosteus aculeatus L.), with some notes on hormonal factors. *Behaviour*, *93*(1), 69–81. doi:10.1163/156853986X00748

Bakker, T. (1986). Aggressiveness in sticklebacks (Gasterosteus aculeatus L.): a behaviour-genetic study. *Behaviour*, *98*(1), 1–114. doi:10.1163/156853986X00937

Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: a study with 16 species of fish. *Laterality*, *5*(3), 269–84. doi:10.1080/713754381

Bisazza, A., Facchin, L., Pignatti, R., & Vallortigara, G. (1998). Lateralization of detour behaviour in poeciliid fish: the effect of species, gender and sexual motivation. *Behavioural Brain Research*, *91*(1-2), 157–64. doi: 10.1016/S0166-4328(97)00114-9

Bisazza, A., Rogers, L. J., & Vallortigara, G. (1998). The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neuroscience and Biobehavioral Reviews*, *22*(3), 411–26. doi:10.1016/S0149-7634(97)00050-X

Bottini, G., & Toraldo, A. (2003). The influence of contralesional targets on the cancellation of ipsilesional targets in unilateral neglect. *Brain and Cognition*, *53*(2), 117–120. doi:10.1016/S0278-2626(03)00091-5

Brown, C., & Braithwaite, V. A. (2004). Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. *Animal Behaviour*, *68*(6), 1325–1329. doi:10.1016/j.anbehav.2004.04.004

Brown, C., Burgess, F., & Braithwaite, V. A. (2007). Heritable and experiential effects on boldness in a tropical poeciliid. *Behavioral Ecology and Sociobiology*, *62*(2), 237–243. doi:10.1007/s00265-007-0458-3

Brown, C., Gardner, C., & Braithwaite, V. A. (2004). Population variation in lateralized eye use in the poeciliid Brachyraphis episcopi. *Proceedings. Biological Sciences / The Royal Society*, *271 Suppl* , S455–7. doi:10.1098/rsbl.2004.0222

Brown, C., & Irving, E. (2014). Individual personality traits influence group exploration in a feral guppy population. *Behavioral Ecology*, *25*(1), 95–101. doi:10.1093/beheco/art090

Brown, C., Jones, F., & Braithwaite, V. (2005). In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, *70*(5), 1003–1009. doi:10.1016/j.anbehav.2004.12.022

Burns, J. G. (2008). The validity of three tests of temperament in guppies (Poecilia reticulata). *Journal of Comparative Psychology (Washington, D.C. : 1983)*, *122*(4), 344–56. doi:10.1037/0735-7036.122.4.344

Cantalupo, C., Bisazza, A., & Vallortigara, G. (1995). Lateralization of Predator-evasion Response in a Teleost Fish (*Girardinus falcatus*). *Neuropsychologia*, *33*(12), 1637–1646. doi:10.1016/0028-3932(95)00043-7

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, *88*, 465–475. doi:10.1111/brv.12007

Champagne, D. L., Hoefnagels, C. C. M., de Kloet, R. E., & Richardson, M. K. (2010). Translating rodent behavioral repertoire to zebrafish (Danio rerio): relevance for stress research. *Behavioural Brain Research*, *214*(2), 332–42. doi:10.1016/j.bbr.2010.06.001

Chang, C., Li, C.-Y., Earley, R. L., & Hsu, Y. (2012). Aggression and related behavioral traits: the impact of winning and losing and the role of hormones. *Integrative and Comparative Biology*, *52*(6), 801–13. doi:10.1093/icb/ics057

Chapman, B. B., Morrell, L. J., & Krause, J. (2010). Unpredictability in food supply during early life influences boldness in fish. *Behavioral Ecology*, *21*(3), 501–506. doi:10.1093/beheco/arq003

Coleman, K., & Wilson, D. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, *56*(4), 927–936. doi:10.1006/anbe.1998.0852

Dadda, M., Domenichini, A., Piffer, L., Argenton, F., & Bisazza, A. (2010). Early differences in epithalamic left-right asymmetry influence lateralization and personality of adult zebrafish. *Behavioural Brain Research*, *206*(2), 208–15. doi:10.1016/j.bbr.2009.09.019

Diekamp, B., Regolin, L., Güntürkün, O., & Vallortigara, G. (2005). A left-sided visuospatial bias in birds. *Current Biology*, *15*(10), 372–373. doi:http://dx.doi.org/10.1016/j.cub.2005.05.017

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *The Journal of Animal Ecology*, *76*(6), 1128–38. doi:10.1111/j.1365-2656.2007.01284.x

Earley, R., Hsu, Y., & Wolf, L. (2000). The use of standard aggression testing methods to predict combat behaviour and contest outcome in *Rivulus marmoratus* dyads (Teleostei: Cyprinodontidae). *Ethology*, *106*(8), 743–761. doi:10.1046/j.1439-0310.2000.00586.x

Espinoza, W. A. S. (2011). *Sexual differentiation, neurobiology, and behaviour in the convict cichlid (Cryptoheros nigrofasciatus)*.

Facchin, L., Bisazza, A., & Vallortigara, G. (1999). What causes lateralization of detour behavior in fish? Evidence for asymmetries in eye use. *Behavioural Brain Research*, *103*(2), 229–34. doi:10.1016/S0166-4328(99)00043-1

Franck, D., & Ribowski, A. (1987). Influences of prior agonistic experiences on aggression measures in the male swordtail (*Xiphophorus helleri*). *Behaviour*, *103*(1), 217–240. doi:10.1163/156853987X00369

Heiligenberg, W. (1965). Colour polymorphism in the males of an African cichlid fish. *Proceedings of the Zoological Society of London*, *146*(1), 95–97. doi:10.1111/j.1469-7998.1965.tb05202.x

Hsu, Y., Earley, R. L., & Wolf, L. L. (2006). Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biological Reviews of the Cambridge Philosophical Society*, *81*(1), 33–74. doi:10.1017/S146479310500686X

Hurd, P. L. (2006). Resource holding potential, subjective resource value, and game theoretical models of aggressiveness signalling. *Journal of Theoretical Biology*, *241*(3), 639–48. doi:10.1016/j.jtbi.2006.01.001

Jakobsson, S., Radesäter, T., & Järvi, T. (1979). On the Fighting Behaviour of Nannacara anomala (Pisces, Cichlidae)♂♂. *Zeitschrift Für …*, *49*, 210–220. doi: 10.1111/j.1439-0310.1979.tb00288.x

Just, W., & Morris, M. R. (2003). The Napoleon Complex: why smaller males pick fights. *Evolutionary Ecology*, *17*(5/6), 509–522. doi:10.1023/B:EVEC.0000005629.54152.83

Kruskal, J.B. & Wish, M. (1978). *Multidimensional scaling*. E. M. Uslander (Ed.). Quantitative Applications in the Social Sciences. Beverly Hills, CA: Sage Publications LTD.

Larson, E. T., O'Malley, D. M., & Melloni, R. H. (2006). Aggression and vasotocin are associated with dominant-subordinate relationships in zebrafish. *Behavioural Brain Research*, *167*(1), 94–102. doi:10.1016/j.bbr.2005.08.020

Linke, H., & Staeck W. (1994) African Cichlids I Cichlids From West Africa: A handbook for their identification, care, and breeding. Melle, Germany: Tetra-Press.

Martin, E., & Taborsky, M. (1997). Alternative male mating tactics in a cichlid, Pelvicachromis pulcher : a comparison of reproductive effort and success. *Behavioral Ecology and Sociobiology*, *41*(5), 311–319. doi:10.1007/s002650050391

Moscicki, M. K., & Hurd, P.L. (2014). *Sex, prior, and current stress exposure affect exploration and behavioural syndromes in convict cichlids (Amatitlania nigrofasciata)*. Manuscript in preparation.

Moscicki, M. K., Reddon, A. R., & Hurd, P. L. (2011). Lateralized behaviour of a non-social cichlid fish (Amatitlania nigrofasciata) in a social and a non-social environment. *Behavioural Processes*, *88*(1), 27–32. doi:10.1016/j.beproc.2011.07.004

Northmore, D. (2011). *Optic Tectum*. *Encyclopedia of Fish Physiology: From Genome to Environment* (Vol. 1, pp. 131–142). Elsevier Inc. doi:10.1016/B978-0-12-374553-8.00093-9

Nwadiaro, C. (1985). The distribution and food habits of the dwarf African cichlid, *Pelvicachromis pulcher* in the River Sombreiro, Nigeria. *Hydrobiologia*, *164*(121), 157–164. doi:10.1007/BF00008719

Ospina-Álvarez, N. & Piferrer, F. (2008). Temperature-Dependent Sex Determination in fish revisited: prevalence, a single sex ratio response patter, and possible effects of climate change. *PLoS ONE*, 3(7). doi: 10.1371/journal.pone.0002837

Reddon, A. R., & Balshine, S. (2010). Lateralization in response to social stimuli in a cooperatively breeding cichlid fish. *Behavioural Processes*, *85*(1), 68–71. doi:10.1016/j.beproc.2010.06.008

Reddon, A. R., & Hurd, P. L. (2008). Aggression, sex and individual differences in cerebral lateralization in a cichlid fish. *Biology Letters*, *4*(4), 338–40. doi:10.1098/rsbl.2008.0206

Reddon, A. R., & Hurd, P. L. (2009). Individual differences in cerebral lateralization are associated with shy–bold variation in the convict cichlid. *Animal Behaviour*, *77*(1), 189–193. doi:10.1016/j.anbehav.2008.09.026

Reddon, A. R., & Hurd, P. L. (2013). Water pH during early development influences sex ratio and male morph in a West African cichlid fish, Pelvicachromis pulcher. *Zoology (Jena, Germany)*, 1–5. doi:10.1016/j.zool.2012.11.001

Robins, A, Lippolis, G., Bisazza, A, Vallortigara, G., & Rogers, L. (1998). Lateralized agonistic responses and hindlimb use in toads. *Animal Behaviour*, *56*(4), 875–881. doi:10.1006/anbe.1998.0877

Römer, U., & Beisenherz W. (1996). Environmental determination of sex in *Apistogramma* (Chiclidae) and two other freshwater fishes (Teleostei). *Journal of Fish Biology*, *48*(4): 714-725. doi: 10.1111/j.1095-8649.1996.tb01467.x

Rubin, D. (1985). Effect of pH on sex ratio in cichlids and a poecilliid (Teleostei). *Copeia*, *1985*(1), 233–235. doi:10.2307/1444818

Scharnweber, K., Plath, M., & Tobler, M. (2011). Examination of boldness traits in sexual and asexual mollies (*Poecilia latipinna*, *P. formosa*). *Acta Ethologica*, *14*(2), 77–83. doi:10.1007/s10211-011-0097-6

Schwartzer, J. J., Ricci, L. A, & Melloni, R. H. (2013). Prior fighting experience increases aggression in Syrian hamsters: implications for a role of dopamine in the winner effect. *Aggressive Behavior*, *39*(4), 290–300. doi:10.1002/ab.21476

Snekser, J. L., & Itzkowitz, M. (2014). Contrasting Parental Tasks Influence Parental Roles for Paired and Single Biparental Cichlid Fish. *Ethology*, *120*(5), 483–491. doi:10.1111/eth.12221

Sovrano, V. a, Bisazza, A., & Vallortigara, G. (2001). Lateralization of response to social stimuli in fishes: a comparison between different methods and species. *Physiology & Behavior*, *74*(1-2), 237–44. doi:10.1016/S0031-9384(01)00552-2

Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A Methodological Review of Personality-Related Studies in Fish: Focus on the Shy-Bold Axis of Behavior. *International Journal of Comparative Psychology*, *23*(1), 1–25.

Uttl, B., & Pilkenton-Taylor, C. (2001). Letter Cancellation Performance Across the Adult Life Span. *The Clinical Neuropsychologist (Neuropsychology, Development and Cognition: Section D)*, *15*(4), 521–530. doi:10.1076/clin.15.4.521.1881

Vallortigara, G. (2000). Comparative neuropsychology of the dual brain: a stroll through animals' left and right perceptual worlds. *Brain and Language*, *73*(2), 189–219. doi:10.1006/brln.2000.2303

Vallortigara, G. (2006). The evolutionary psychology of left and right: costs and benefits of lateralization. *Developmental Psychobiology*, *48*(6), 418–427. doi:10.1002/dev.20166

Vallortigara, G., Rogers, L., Bisazza, A., Lippolis, G., & Robins, A. (1998). Complementary right and left hemifield use for predatory and agonistic behaviour in toads. *Neuroreport*, *9*(14), 3341–3344. Retrieved from http://journals.lww.com/neuroreport/Abstract/1998/10050/Complementary_right_and_left_hemifield_use_for.35.aspx

Webb, C. E., Franks, B., Romero, T., Higgins, E. T., & de Waal, F. B. M. (2014). Individual differences in chimpanzee reconciliation relate to social switching behaviour. *Animal Behaviour*, *90*, 57–63. doi:10.1016/j.anbehav.2014.01.014

Wong, M., & Balshine, S. (2011). Fight for your breeding right: hierarchy re-establishment predicts aggression in a social queue. *Biology Letters*, *7*(2), 190–3. doi:10.1098/rsbl.2010.0639