THE PENNSYLVANIA STATE UNIVERSITY SCHREYER HONORS COLLEGE

DEPARTMENT OF BIOLOGY

SHOALING BEHAVIOR AND BOLDNESS IN GUPPIES DESCENDED FROM HIGH AND LOW PREDATION POPULATIONS

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A thesis submitted in partial fulfillment of the requirements for a baccalaureate degree in Veterinary and Biomedical Science with honors in Biology

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ABSTRACT

This experiment examined the behavioral and cognitive traits impacted by predation pressure using female guppies descended from fish originally obtained at high and low predation sites from rivers in Trinidad. Previous studies have shown that guppies will preferentially shoal with larger groups, and are able to differentiate between groups of two and three fish. We evaluated the impact of high and low predation ancestry and temperament on the ability to, and preference for, selecting a larger shoal. Domesticated guppies were also evaluated for these traits and compared to those descended from wild-caught fish. Temperament was assessed using an open field trial prior to shoaling trials to determine whether the fish preferred to shoal with a group of two guppies or a group of three guppies. We hypothesized that the different populations would vary in their temperament, and that temperament would affect shoaling preferences. We also predicted that shoaling preference in high predation descendants would be to shoal with the larger group because it provides protection from predators (Seghers 1974). The temperament trials showed there was no difference in the boldness of the high and low predation populations and the domestic guppies, nor were there population differences in shoaling behaviors. Our results did show, however, that bolder guppies spend less time shoaling with the larger group, and prefer smaller groups of conspecifics. Due to the small sample size, additional trials are needed to confirm that there are no population differences in temperament or shoaling behavior between these groups. This will indicate whether shoaling behavior is strongly selected for in nature or whether the shoaling preferences are lost when animals are removed from a pressured environment.

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INTRODUCTION

System for small quantity discrimination

Several studies have determined that two non-verbal systems for comparing numerosities exist in both humans and non-human animals. While this has primarily been studied in primates and infants, it also exists in less complex, phylogenetically older species suggesting is has an "ancient phylogenetic origin" (Agrillo et al. 2009). Fish possess these two systems for quantity discrimination: one for small numbers and one for large numbers (Bisazza et al. 2010, Agrillo et al. 2012). This experiment evaluated the ability of the guppy (*Poecila reticulata*) to discriminate between small quantities to investigate shoaling behavior. The mechanism is an object-tracking system that tracks individual elements (Agrillo et al. 2008). Because this system is limited by the capacity of the guppy's working memory, it is only able to track 4 objects at once. Using this mechanism, fish are able to discriminate between shoaling groups that differ by one element such as 1 vs. 2, 2 vs. 3 and 3 vs. 4. This trait has been demonstrated in guppies as young as one day old suggesting it is an innate ability (Bisazza et al. 2010). Above four elements, fish are not able to accurately discriminate between them unless they are 1:2 or smaller ratios apart (Agrillo et al. 2012). There is the potential that fish could use non-numerical variables to help distinguish between groups, such mechanisms could include luminance, total surface area, or overall space occupied. When Agrillo et al. (2009) controlled for these variables and trained mosquitofish (Gambusia holbrooki) to select between images of 2 or 3 objects, they found that the fish still significantly selected for their trained number. Therefore, fish can use numbers when other continuous variables are excluded (Agrillo et al. 2009). In natural environments, there are advantages to being able to discriminate between quantities. For example, lions decide whether

or not to attack another group based on a comparison of the number of roaring individuals between the invading group and their own (Agrillo et al 2009). It is also advantageous for fish to be able to distinguish between quantities in order to shoal with larger groups as an antipredator response, within larger groups predation risk is dispersed among more individuals and each fish reduces its individual risk (Magurran et al. 1985).

Advantages and disadvantages of shoaling

In addition to attenuating predation risk, shoaling offers several advantages. For example, shoaling allows fish to maintain vigilance for predators while foraging for food, a task that is more difficult to perform alone or even in a small group. Magurran et al. (1985) demonstrated that minnows (*Phoxinus phoxinns*) in large shoals reduced their foraging time but fed on food patches for longer periods of time. The fish in the experiment displayed an increased detection distance but a decreased flight distance than smaller shoaling groups (Magurran et al. 1985). This allows the fish to balance the demands of foraging and predator defense. Furthermore, shoaling allows the prey to confuse the predator and reduce the likelihood of a successful attack. Certain maneuvers within the shoal can even reduce an individual's chance of being captured (Fuiman and Magurran 1994).

Guppies can gain many advantages from shoaling but these must be balanced with other constraints such as increased competition; shoaling is a dynamic behavior and is context-dependent (Hoare et al. 2003). Shoaling helps guppies forage for food while maintaining vigilance for predators. These benefits typically increase with the size of the group (Hoare et al. 2003). However, with increased shoal size also comes increased competition for resources. Therefore, shoaling is most advantageous when the threat of predation is high and resources are abundant. Hoare et al. showed that when killifish (*Fundulus diaphanus*) are presented with food,

group size decreased and 60% of fish were found alone compared to 36% in control studies. Furthermore, food deprived fish show a reduced tendency to shoal with large groups. In addition, when the fish were presented with chemical cues indicating the successful attack of a predator, they formed the largest groups possible. In this scenario, more than 60% of individuals formed shoals of 10 (Hoare et al. 2003). This reinforces that while shoaling with large groups may be beneficial at times of high predation, it also causes competition in the presence of food. Shoaling provides fish with a greater chance of survival in areas of high predation so it would make sense that different populations may develop different shoaling behavior.

Temperament and environment

Like humans, fish display a continuous range of personalities (Brown et al. 2005). One common measurement of temperament in numerous taxa, including humans, is the scale of boldness and shyness (Brown et al. 2005). The temperament of animals is often a result of selection pressure from the environment (Harris et al. 2010, Bell and Sih 2007). This correlation depends on the selective pressure in the region and the behavioral plasticity (Harris et al. 2010). Under the threat of predation, this continuum elicits a variety of responses in prey species; those that choose the stay hidden do so at the cost of lost mating and feeding opportunities while those that take risks increase their chance of detection by predators (Harris et al. 2010). A study using *Brachyraphis episcopi* from high and low predation sites found that the boldness of the fish increased as the level of predation increased; conversely the fish from the lower predation sites were found to be more timid (Brown et al. 2005).

Aripo and Naranjo River populations

The Aripo and Naranjo Rivers in Trinidad allow researchers the unique opportunity to study guppies (*P.reticulata*) that have been separated into a high predation and low predation populations. In the Northern Range Mountains in Trinidad, tributaries vary in their intensities of predation level. Two of these rivers, the Naranjo (Upper Aripo) and Aripo (Lower Aripo), are separated by a waterfall that prevents predator fish such as characids and cichlids from moving upstream (Seghers 1974). With the exception of predators, the rivers do not differ strongly in other aspects. This creates two separate populations of guppies, one in the Naranjo River that experience low predation and one in the Aripo River that experience high predation. This selection pressure can generate a divergence in behavior between the fish that differ in their predation levels (Archard et al. 2012, Bell and Sih 2007). Studies have shown that fish descended from wild populations from the Aripo River show more pronounced shoaling behavior than those descended from the Naranjo River, and this shoaling behavior was also found to increase the chances of surviving predation (Seghers 1974). The fish used in this thesis were descendants of the Aripo River and Naranjo River and therefore are predicted to express similar shoaling responses as those reported by Seghers (1974).

Domesticated guppies

In contrast to the predation pressure put on the wild-caught descendants, the domesticated guppies included in the experiment were only selected for their attractive colors. Guppies in the wild display a color pattern that is a balance between predator avoidance and sexual selection (Endler 1980). With the artificial selection for color, these fish have lost their naturally selected traits. Therefore, they are expected to behave differently.

Predation pressure

Predation pressure can be a strong selective force on populations. In fact, predation of *P.reticulata* has influenced a variety of morphologic and behavioral traits (Farr 1974, Godin 1995, Ardent and Reznick 2005). These mechanisms can either be through the direct effect of predation or non-lethal effects (Lima 1998). Therefore it is reasonable to expect a difference in behavior between the high predation Aripo River population and the low predation Naranjo River population. However, this experiment tests the descendants of these populations and will test the persistence of shoaling behavior in the absence of predation.

Hypothesis

We hypothesized that fish descended from the wild caught high predation Aripo River population would have an increased preference for a larger shoaling group than those descended from the low predation Naranjo River population. Furthermore, we hypothesized that the populations would differ in their temperament, specifically boldness and shyness. Domesticated guppies with no predation experience were used as a comparison to these populations.

MATERIALS AND METHODS

Three populations of guppies were evaluated during this study; one from the high predation Aripo River, one from the low predation Naranjo River, and domesticated guppies originally obtained from hobby breeders where the fish were selected for exaggerated color traits. These populations were maintained in separate tanks from which adult-sized females were randomly drawn for experiments. The experiment utilized 16 female domesticated guppies, 10 female Aripo River descendants and 10 female Naranjo River descendants. The fish were housed in a basement room of the Forest Resources Building which was kept at a temperature of 68°F in a 12 hour light and 12 hour dark cycle. They were provided with standard fish flakes and brine shrimp on a daily basis, artificial plants, and maintained at a water temperature of roughly 72-76°F using a heater. Water filters in the tanks maintained a clean environment and aerate the water. The IACUC approval number for this experiment is 36902.

Temperament assessment

Individual fish were transferred from their holding tank to an open field trial tank using a small net, which was an opaque arena 30 x 40 x 24 cm, with 15 cm water depth. The bottom of the tank was marked with a grid and a separate line to distinguish between the center and edge of the tank. The test fish was kept in a clear start cylinder in the center of tank for 5 minutes and allowed it to settle. The cylinder was then raised remotely by the experimenter from behind an opaque curtain and the trial began. An overhead camera filmed the fish for 5 minutes, as measured by a stopwatch, as the fish swam around the new environment. After completing the 5 minute recorded trial, the fish was allowed to rest in the open field trial tank for 10 minutes. The

numbers of grid lines crossed, the total time spent in the center of the tank, and the latency to first cross to the edge were measured to provide an indication of boldness and activity level of the guppy. The computer program Etholog v2.2.5 was used to help summarize these measurements using the videos.

Shoaling behavior trials

The fish was then moved to the numerosity tank where it was held in another clear cylinder for 2 minutes. The numerosity tank consisted of two end sections partitioned off with clear Plexiglas and the center section in which the test fish is placed. Groups of two and three guppies were placed in either end so the test guppy could observe but not reach them. Left and right preference was avoided by switching which side tank the shoaling group of 2 or 3 was placed. Lines marking a 10 cm distance from the end sections were used to determine if the test fish were close enough to interact with the groups. The experimenter released the test guppy by raising the cylinder, which began the 15 minute recorded trial. The camera was fixed on a tripod to minimize observer interference. After the trial, the test guppies were placed in tanks for fish that had completed trials according to their population. Upon review of the video, the time the test guppy spent within the 10 cm mark of each group of conspecifics was recorded to quantify their preference for shoaling with 2 or 3 fish.

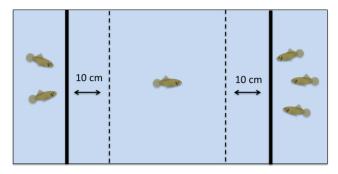


Figure 1: Shoaling trial tank set up with a middle tank for the test fish and two side tanks for the shoaling groups

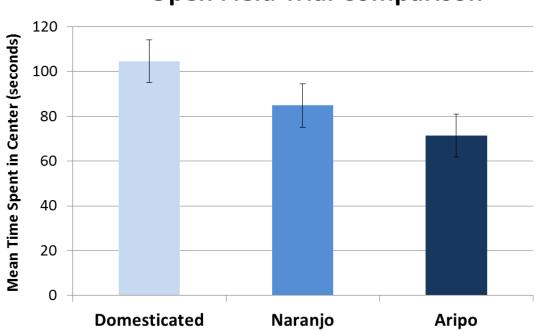
Statistical analysis

All statistical analysis was performed using SPSS computer software. Frequencies were arcsine square root-transformed and times were log transformed. The open field trial and shoaling trial data were analyzed using a one-way analysis of variance (ANOVA) test. A Pearson's correlation test was used to investigate if there was a relationship between boldness and shoaling preferences. A 2-tailed paired t test was performed on the combined populations to compare the percent of time spent with 2 fish and the percent of time spent with 3 fish.

RESULTS

Open field trial

The open field trial data for each population is summarized in the tables of Appendix A. Statistical analysis shows that the populations displayed no difference in behaviors of the fish in the open field trial. The one-way ANOVA test showed that there was no difference in the time spent in the center (M = 4.40; SD = 1.08; df = 2; $F_{(2,33)} = 1.581$; p = 0.221), the time frozen (M = 0.419; SD = 0.421; df = 2; $F_{(2,33)} = 0.931$; p = 0.404) or the number of lines crossed (M = 4.62; SD = 0.579; df = 2; $F_{(2,31)} = 1.37$; p = 0.269). Therefore, the fish did not differ in their boldness or activity levels. A larger sample size may show greater differences in temperament between domesticated and wild-caught descendants. This data is illustrated by Figure 2 below.



Open Field Trial Comparison

Figure 2: Analysis of the open field trial behavior shows no differences between the domesticated population, Naranjo River descendants and the Aripo River descendants.

Shoaling behavior trial

The shoaling behavior trial data is summarized for each population in the tables of Appendix A. The percent of time spent with 2 fish and 3 fish was analyzed for each population separately. The ANOVA test showed that there were no population differences for the preference of the group of 2 or 3 fish; therefore, the populations were combined and the data was pooled. Similarly, when the populations were combined, the percent time the fish spent with the group of 2 (M = 0.629; SD = 0.488; df = 2; $F_{(2,35)} = 0.205$; p = 0.816) and the group of 3 fish (M = 0.419; SD = 0.421; df = 2; $F_{(2,35)} = 1.147$; p = 0.330) was not significant as demonstrated by Figure 3 below.

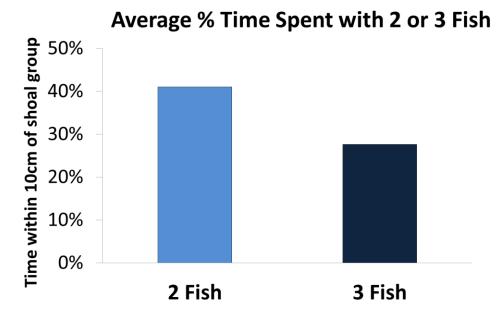


Figure 3: The percent of time spent with 2 fish or 3 fish during the shoaling behavior trials did not differ between populations. The percent of time the combined populations spent with the group was not significant.

In addition, a univariate ANOVA of the proportion of the time spent on the left (M = 0.447; SD = 0.442; df = 2; $F_{(2,35)} = 0.815$; p = 0.451), right (M = 0.642; SD = 0.488; df = 2; $F_{(2,35)} = 1.450$; p = 0.249) and in the middle (M = 0.575; SD = 0.324; df = 2; $F_{(2,35)} = 0.915$; p = 0.410) were not significant; this shows that the fish did not have a significant preference for the left or right side tanks which housed the shoaling groups.

A paired t test was performed on the combined populations to compare the percent of time spent with 2 fish and the percent of time spent with 3 fish (M = -0.210; SD = 0.796; df = 35; t = -1.585; p 2-tailed = 0.122). The percent of time spent with 3 fish negatively correlated with the time the fish spent in the center of the open field trial tank (p 2-tailed = 0.014, Pearson Correlation = -0.408). This shows that the bolder the fish, the less likely they were to shoal with the larger group. The results of the correlation tests from SPSS are illustrated in Figure 4 below.

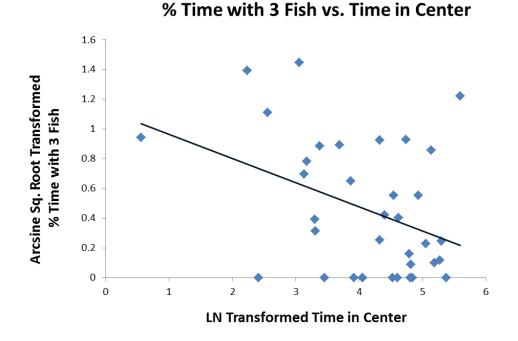


Figure 4: A negative correlation between the percent of time spent with 3 fish in the shoaling trial and the time spent in the center of the open field arena show that bolder fish are less likely to shoal with the larger group.

DISCUSSION

Boldness and shoaling behavior

The results from this experiment show that there are no differences in the boldness or shoaling preferences between the domesticated and wild-caught descendants. By combining the populations, it was revealed that the bolder the fish is, the less time they spent with the larger shoaling group. Previous studies indicate that guppies prefer to shoal with the larger group during the threat of predation (Hoare et al. 2003). In this thesis, boldness was measured by the amount of time spent in the center of the open field trial tank. Entering the center of the open field arena is considered to be bold because fish are exposed and vulnerable in an unfamiliar environment. Open field trials have been used as a measurement of boldness and exploratory activity for a variety of species by observing the animal's behavior while in the novel arena (Burns 2008). Therefore, it is logical that bolder fish with less fear of predation would avoid shoaling with the group of three fish. Without the threat of predation, fish avoid larger shoals in favor of smaller ones to avoid competition (Hoare et al. 2003). Not only does shoaling give the prey the advantages of increased vigilance and predator detection, but it also gives the predator the disadvantage of a less successful attack (Magurran 1990). However, this comes with increased competition and when fish are hungry and form smaller groups when in the presence of food (Hoare et al. 2003).

Original predictions

The hypothesis addressing the relationship between shoaling and population were not confirmed by the results. It must be considered that the lack of a result is a consequence of a small sample size. The original predictions are based on evidence of shoaling behavior in the presence of predation and ancestral environments of the guppies. According to original predictions, the Aripo River descendants would have a higher preference for the larger shoaling group for protection due to ancestral predation pressure. Therefore, the Naranjo River descendants would prefer the smaller shoaling group to avoid competition for food and mates because they lack the perceived threat of predation the Aripo River descendants possess. In comparison, it was predicted that the domesticated guppies would have a strong preference for the smaller shoaling group because they experienced the highest level of competition and are farthest removed from the threat of predation. Similarly, it was hypothesized that the Aripo River guppies would be bolder than the Naranjo River descendants.

Evidence for heritability of shoaling behavior in P.reticulata

Another explanation of our results is that shoaling behavior is not heritable in guppies. However, previous studies suggest there is a genetic component to shoaling behavior in *P.reticulata* due to the conserved shoaling behavior from their wild counterparts (Seghers 1974, Huizinga et al. 2009). Huizinga et al. (2009) propose that shoaling in guppies is a result of genetic accommodation of a trait that is environmentally induced and some aspects of the guppies' antipredator behaviors are learned whereas others are genetically inherited. The social environment, such as the density of fish, during rearing has been demonstrated to influence shoaling behavior in lab-reared fish (Song et al. 2011, Chapman et al. 2008). Furthermore, social learning may accentuate the genetically predisposed shoaling behavior (Song et al. 2011). Due to the evidence of genetic influence on the shoaling behavior of guppies, it is unlikely that our results suggest that shoaling is not an inherited trait but may indicate that the housing conditions are influencing the phenotypes of the guppies.

Recommendations for future research

The experimental set up was able to provide fish with a choice between two shoaling groups. However, this experiment showed no differences in shoaling preference or temperament between the test populations; this could either indicate that there are no differences or that a larger sample size is needed to reveal those differences. Previous studies investigating the temperament of *B. episcopi* from high and low predation sites found that fish from high predation populations were bolder and more active, suggesting that our results are due to a small sample size (Archard et al. 2012). Furthermore, it might provide an interesting comparison to include the original wild guppy populations from the Aripo and Naranjo Rivers. The information provided by analyzing these populations would show how the behavior is expressed in wild individuals and whether that changes in a laboratory environment.

Additionally, trials to compare the shoaling preference between groups of larger quantities of fish could provide an insight into whether the shoaling behaviors rely more on the system for discrimination between large quantities than the system for small quantities. In this set up, the appropriate ratios should be taken into consideration as they need to be 1:2 or smaller for the fish to be able to accurately discriminate between the groups (Bisazza et al. 2010, Agrillo et al. 2012). Furthermore, the fish used for this variation of the experiment should be of adult age since this ability does not develop until later in life (Bisazza et al. 2010).

In conclusion, this experiment showed that there is no significant difference between the shoaling behaviors of domesticated, Aripo River, and Naranjo River guppies. However, bolder guppies were found to be less likely to shoal with the larger group.

APPENDIX A

Summarized Data Tables

Fish Number	Lines Crossed	Time in Center	Time at Edge	Time Frozen
1	117	124.1	165.56	10.34
2	195	92.5	164.44	43.06
3	197	120.9	173.07	6.03
4	40	195.21	26.29	78.5
5	145	179.71	89.18	31.11
6	90	102.15	140	57.85
7	151	100.3	135.89	63.81
8	85	200.52	52.87	46.61
9	146	81.82	159.17	59.01
10	75	127.11	110.07	62.82
11	26	27.47	83.27	189.26
12	295	57.64	242.36	0
13	22	9.33	58.35	232.32
14	93	156.31	120.45	23.24
15	70	75.53	199.02	25.45
16	55	21.23	252.64	26.13
Average	112.63	104.49	135.79	59.72

 Table 1-1: Domesticated female open field trial data

Fish Number	Lines Crossed	Time in Center	Time at Edge	Time Frozen
1	159	29.35	230.99	39.67
2	75	94.52	73.38	132.10
3	165	27.1	184.01	88.89
4	87	270.43	8.26	21.35
5	181	47.87	252.13	0.00
6	131	11.14	265.37	23.49
7	118	115.02	126.51	57.96
8	141	40	243.8	16.20
9	0	1.74	0	298.96
10	184	75.94	162.34	61.72
Average	124.10	71.31	154.68	74.03

 Table 1-2:
 Aripo River female open field trial data

 Table 1-3:
 Naranjo River female open field trial data

Fish Number	Lines Crossed	Time in Center	Time at Edge	Time Frozen
1	160	139.49	154.62	5.89
2	125	170.73	86.44	42.83
3	55	215.80	22.16	62.04
4	149	22.84	229.29	49.87
5	121	31.61	194.67	76.68
6	104	57.50	175.62	66.88
7	1	23.96	0	276.04
8	52	12.86	156.97	130.17
9	78	50.37	97.13	152.50
10	68	122.97	88.78	88.25
Average	91.30	84.81	120.57	95.12

 Table 2-1: Domesticated female shoaling trial data

Fish Number	Percent Time in Middle	Percent Time with 2 Fish	Percent Time with 3 Fish
1	9.43%	89.80%	0.77%
2	38.61%	61.39%	0.00%
3	55.78%	41.67%	2.55%
4	97.88%	0.79%	1.33%
5	17.27%	81.76%	0.97%
6	22.56%	62.22%	15.22%
7	100.00%	0.00%	0.00%
8	5.46%	88.71%	5.84%
9	48.01%	35.37%	16.62%
10	4.64%	95.36%	0.00%
11	65.38%	25.17%	9.45%
12	60.30%	39.70%	0.00%
13	3.15%	0.00%	96.85%
14	51.47%	43.48%	5.05%
15	25.55%	10.92%	63.53%
16	1.54%	0.00%	98.46%
Average	37.94%	42.27%	19.79%

 Table 2-2:
 Aripo female shoaling trial data

Fish Number	Percent Time in Middle	Percent Time with 2 Fish	Percent Time with 3 Fish
1	18.76%	21.54%	59.70%
2	7.36%	64.98%	27.66%
3	11.88%	73.65%	14.46%
4	11.83%	0.00%	88.17%
5	24.34%	39.09%	36.57%
6	6.32%	93.68%	0.00%
7	35.80%	0.00%	64.20%
8	39.46%	0.00%	60.54%
9	31.20%	3.36%	65.43%
10	40.57%	53.16%	6.27%
Average	22.75%	34.95%	42.30%

Fish Number	Percent Time in Middle	Percent Time with 2 Fish	Percent Time with 3 Fish
1	33.66%	38.72%	27.62%
2	43.12%	0.00%	56.88%
3	15.07%	84.93%	0.00%
4	48.08%	10.75%	41.17%
5	56.08%	43.92%	0.00%
6	10.49%	89.51%	0.00%
7	50.36%	0.00%	49.64%
8	19.88%	0.00%	80.12%
9	1.67%	98.33%	0.00%
10	15.48%	84.52%	0.00%
Average	29.39%	45.07%	25.54%

 Table 2-3: Naranjo female shoaling trial data

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Education

B.S. in Veterinary and Biomedical Science Pennsylvania State University, University Park, PA Schreyer Honors College Expected Graduation Date: Spring 2014

School of Veterinary Medicine, University of Pennsylvania Expected Matriculation Date: Fall 2014

Honors and Awards

Dean's List, 2010-2014 \$1,546 College of Agriculture Undergraduate Research Grant 2014 \$1,000 annual scholarship from Doylestown Rotary Club \$1,500 annual scholarship from Schreyer Honors College \$2,000 annual scholarships from College of Agricultural Sciences

Association Memberships/Activities

Braithwaite Lab Group 2012-Present Penn State Pre-Vet Club 2010-2012 Penn State Student Chapter of the Wildlife Society 2010-2012 Small and Exotic Animals Club 2010-2011 Penn State Equine Research Team 2010-2011

Professional Experience

Shadowed vet at Main Street Animal Hospital, 200 hrs Shadowed vet at Eastern Oregon Animal Health, 50 hrs Shadowed vet at Doylestown Animal Medical Clinic, 100 hrs Attended APVMA Symposium, 2012 University of Pennsylvania Summer VETS Program, 2012 Rotations at Ryan-VHUP: Oncology, Medicine

Professional Presentations

Presented at Gamma Sigma Delta Research Expo 2014