4-29-2021

# The Effect of Color Morph on Behavior Interactions in Red-backed Salamanders (Plethodon cinereus)

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# The Effect of Color Morph on Behavior Interactions in Red-backed Salamanders (*Plethodon cinereus*)

by

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Honors Thesis

Submitted to:

Biology Department

University of Richmond

Richmond, VA

April 29, 2021

Advisor: Dr. Kristine Grayson

This thesis has been accepted as part of the honors requirements in the Department of Biology.

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28 April 2021

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27 April 2021

(date)

**Abstract**

Studies in behavioral ecology provide critical information regarding a species' territoriality, predator-prey interactions, and reproduction. Red-backed salamanders (*Plethodon cinereus*) are a polymorphic terrestrial amphibian whose behavioral interactions have long been studied to provide insights on the processes that structure salamander populations, which are often cryptic and difficult to study. However, research regarding the effect of coloration on these interactions is more limited, but potentially extremely important for studies of population dynamics and speciation in terrestrial salamanders. In this study, aggressive and submissive behaviors of adult male red-backed salamanders in five different color morph treatment pairings were observed to determine if differences in aggressive behavior are correlated with color morph. The effects of environmental conditions and size on aggressive and submissive behavior were also measured. There was no significant difference in aggression index between the color morphs, or between any of the treatment pairs. Pairing treatment had a significant effect on the duration of laying next to the other salamander, but the low sample size of salamanders that displayed this behavior may have skewed this result. Salamanders collected from cover boards with multiple adults underneath had significantly higher aggression indices than salamanders collected from boards with no other adults present. Sky conditions also had a significant effect on aggression index, but a low sample size of salamanders collected during certain conditions suggests that more research is needed on the relationship between weather conditions and behavior. This study's findings contradict past research that found differences in aggressive behavior between color morphs, which indicates that salamanders in different populations and/or regions may display different behaviors. Future amphibian research and conservation efforts should thus be aware of potential population-specific behaviors within a species.

## Introduction

The field of behavioral ecology bridges the study of animal behavior with evolutionary biology to investigate how behavior affects fitness (Gordon 2011). One phenomenon that has been particularly studied is how animal behavior is affected by coloration, particularly in conspicuous taxa such as birds and fish. Observing behavioral differences between different color morphs of the same species can provide insight into that species' ecology; prior studies on color morph behavioral differences have included such diverse topics as aggression in a Brazilian lizard, anti-predator behavior in goldfish, and thermoregulatory behavior in springbok (Bruinjé et al. 2019; Katz et al. 2015; Hetem et al. 2009). Coloration is also important to study in more cryptic taxa, where important interactions often occur out of the typical view of researchers. For terrestrial amphibians that spend much of their underground, the red-backed salamander (*Plethodon cinereus*) has been an important species for studying behavioral interactions. The two most common color morphs of this widespread species provide an opportunity to test the role of coloration in salamander behavioral ecology.

The red-backed salamander is a terrestrial lungless salamander native to eastern North American forests spanning from southern Quebec to North Carolina (Anthony and Pfingsten 2013). Red-backed salamanders are polymorphic for color; the "striped" morph has a red stripe on the dorsal side, while the "lead" morph has a dark dorsal surface. Due to the wide distribution of plethodontid salamanders and their high relative abundance, they serve as indicators of biodiversity and ecosystem health in forests (Welsh and Droege 2001). This is of particular importance due to the ongoing amphibian extinction crisis, in which 32.5% of amphibian species are threatened with extinction, and between 9 and 122 species are estimated to have gone extinct since 1980 (Mendelson et al. 2006). Additionally, red-backed salamanders exhibit social behaviors to communicate with members of the same species through both visual displays and chemical signals (Jaeger and Forester 1993). Red-backed salamander behavior displayed in laboratory settings can be representative of behavior in the natural environment, which makes laboratory-based studies viable for testing behavioral hypotheses under controlled, replicated conditions (Gergits and Jaeger 1990).

Prior research has sought to determine which factors influence red-backed salamander behavior, and has identified several visual behaviors that indicate either aggression or submission (Jaeger 1984). Furthermore, males are more submissive towards females than towards other males, while females display the same behavior towards both male and other female salamanders (Jaeger 1984). Age appears to play another role in behavior; adult male salamanders are more tolerant of juvenile male intruders to their territory than adult male intruders (Jaeger et al. 1995). Kin recognition was proposed as a possible mechanism responsible for this result, as adults are more tolerant of juveniles with whom they had previously cohabitated with. Additionally, male adult salamanders are less aggressive towards female adults they are familiar with, while female adults are more submissive towards male adults they are familiar with (Guffey et al. 1998). It is theorized that this behavior allows males to increase their opportunities to breed.

The degree to which color morph affects behavior has also been studied. Studies conducted on whether assortative mating based on morph occurs concluded that assortative mating is taking place, but not enough such that speciation between the morphs is likely (Anthony et al. 2008; Acord et al. 2013). Interestingly, striped males are more attractive than lead males to both striped and lead females (Acord et al. 2013). Striped salamanders have more diverse and higher quality diets than lead salamanders, and retreat from the surface later than lead salamanders when temperatures drop in autumn (Anthony et al. 2008). A greater proportion of striped salamanders are territorial residents beneath cover objects compared to the proportion of lead salamanders that are territorial residents, and striped salamanders display longer residency times (Reiter et al. 2014). In a laboratory experiment conducted simultaneously, striped residents displayed more aggressive behavior and less submissive behavior towards intruders than lead residents. While these results suggest that striped salamanders are more aggressive, the experiments were all in the context of territorial behavior. The majority of studies have also been conducted with salamanders collected from the mountains of Virginia and other cool climate locations. In this study, I tested red-backed salamander aggression in a neutral environment to determine the effect of morph on aggressive and submissive behavior. I hypothesized that, in line with past studies, striped salamanders would display more aggressive behavior than lead salamanders. I also conducted my research in a more southern population from the warmest part of the red-backed salamander geographic range, where activity and behavior may differ from cooler climate populations (Hernández-Pacheco et al. 2019).

## Methods

### *Study Area*

Red-backed salamanders were collected from the James River Park system in Richmond, Virginia near the 42nd Street entrance. The study area is a mixed temperate forest located between the James River and suburban housing, and was formerly a mining quarry in the early 1900s. There are 6 artificial cover board plots in the park, consisting of 50 wooden cover boards (1 $ft^2$) arranged in a 5 by 10 m layout. This study was conducted at the F1 plot, located in the base of the quarry, which has not been consistently monitored as part of the long-term mark-recapture study at the site.

*Field Collection*

Salamanders were collected during October-November 2020 and late January-February 2021. Adult *P. cinereus* were collected from beneath cover boards and placed into plastic containers (709mL) with a moist paper towel. Containers were placed in insulated bags and transported to the University of Richmond for behavioral trials. Each container held one salamander, and no more than one salamander was taken from each cover board. A total of approximately 20 salamanders (10 striped and 10 lead) were collected each week. Adult salamanders found alone under a board, or with only juveniles were preferred. If these conditions could not be met during a given sampling occasion, a note was made if the salamander was collected from a board with other adult salamanders present. Environmental conditions were also recorded: air temperature (°C), soil temperature (°C), leaf litter height (cm), wind condition (Beaufort scale range 0-12), sky condition (range 0 no clouds-8 snow; adapted from SPARCnet 2015), and the presence of rain within the past 24 hours (Table 1, 2). Collected salamanders were sexed in the lab, and only males were selected for testing to remove the effect of sex on behavior. Males had their mass (g), snout-to-vent length (mm), and total length (mm) measured. The selected males and the unselected salamanders were then placed back into their containers and stored inside refrigerated chambers (12-15°C, reflecting variable field conditions).

*Behavioral Trials*

I examined the behaviors displayed by three different morph pairings: two striped salamanders (Both Striped), two lead salamanders (Both Lead), and one striped and one lead salamander (Striped and Lead). Additionally, there were two control groups: one lone striped salamander (Striped Control), and one lone lead salamander (Lead Control), which were examined along with a "surrogate salamander," a wet paper towel roughly the size of a salamander (similar to Reiter et al. 2014). The selected two salamanders were removed from the refrigerated chamber and given 5 minutes to adjust to room temperature. The two salamanders were then removed from their respective containers and placed into a large plastic container (6.6L) with a moist paper towel. The salamanders were observed for 15 minutes with behaviors recorded using the BORIS ethogram software v. 7.9.19 (Friard and Gamba 2016). The examined behaviors were: Look Towards, Look Away, Move Towards, Move Away, Raise Trunk, All Trunk Raised, Walk Around Perimeter, Lay Flat, Climb Out, Lay Next to Each Other, and Bite, which were identified by Jaeger et al. (2016b) as aggressive or submissive behaviors (Table 3). After the observation period was finished, a cover board section ($10cm^2$) was placed inside the shared container, and the shared container was placed back into the refrigerated chamber. Approximately 48 hours later, the positions of the two salamanders relative to the cover board was recorded, and all salamanders were returned to the James River Park plot.

*Data analysis*

To create a measure of the overall aggression of each salamander, an aggression index (AI) was calculated as submissive behaviors subtracted from aggressive behaviors ([MT+LT]-[MA+LA]) (Reiter et al. 2014). One-way ANOVA tests were used to determine if AI and behavior durations or frequencies varied across the five treatment groups, as well as if the presence of multiple adults beneath a cover board during collection and position relative to the cover board after completing the behavioral trial corresponded to any difference in AI. Additionally, salamanders were subset into lead and striped to determine if treatment had an effect on just one morph. Correlation tests were performed using Pearson correlation method to evaluate if environmental conditions, time, or size influenced salamander behavior (all statistical analyses were performed in R version 4.0.2, RStudio version 1.3.1073).

## Results

### *Collection data*

A total of 64 salamanders were collected throughout the study: 36 lead and 28 striped. There were 18 salamanders in the Both Lead treatment group, 14 salamanders in the Both Striped treatment group, 16 salamanders in the Striped and Lead treatment group, 10 salamanders in the Lead Control treatment group, and 6 salamanders in the Striped Control treatment group. 32 trials occurred between October-November 2020 and 8 trials occurred in late January-February 2021.

### *Morphological effects on behavior*

Salamanders in the Both Lead treatment had a mean AI of 49.8 ± 16.8 SE. Salamanders in the Both Striped treatment had a mean AI of 89.4 ± 27.8 SE. Salamanders in the Striped and Lead treatment had a mean AI of 60.1 ± 20.8 SE. Salamanders in the Lead Control had a mean AI of 18.9 ± 20.7 SE. Salamanders in the Striped Control had a mean AI of 62.4 ± 68.3 SE. Treatment did not have a significant effect on AI ($p=0.343$; Figure 1). Treatment had a narrowly significant effect on Lay Next To Other (p=0.0484), but a Tukey HSD test did not reveal any significant relationships between treatments (Figure 2). Treatment did not have a significant effect on the durations of Move Towards (p=0.375), Look Towards (p=0.395), Move Away (p=0.502), Look Away (p=0.478), Raise Trunk (p=0.468), Walk around Perimeter (p=0.269), or Lay Flat (p=0.265), or the frequencies of Bite (p=0.271) and Climb Out (p=0.0769).

Morph did not have a significant effect on AI (p=0.073; Figure 3). Salamanders were subset into lead and striped to determine if treatment had an effect on just one morph. Treatment did not have a significant effect on the AI of lead salamanders (p=0.543). Treatment also did not have a significant effect on the AI of striped salamanders (p=0.798). Morph also did not have a significant effect on whether a salamander was beneath a cover board in the testing container (p=0.319), nor did treatment (p=0.923).

*Salamander trait effect on behavior*

Salamanders collected from boards with other adults present had a significantly higher (p=0.0294) AI than salamanders collected from boards with no other adults present (Figure 4). There was no significant difference in AI due to snout-to-vent length (p=0.7838), total length (p=0.2668), or mass (p=0.4369). Additionally, salamander positioning relative to a cover board in the laboratory did not have a significant effect on AI (p=0.429).

*Environmental effects on behavior*

Sky conditions had a significant (p=0.0243) effect on AI (Figure 5). There was no significant difference in AI due to air temperature (p=0.149), soil temperature (p=0.201), leaf depth (p=0.371), wind conditions (p=0.892), or recent rainfall (p=0.098).

**Discussion**

Prior studies have suggested that red-backed salamander color morphs exhibit behavioral differences in mating and territoriality (Anthony et al. 2008; Acord et al. 2013; Reiter et al. 2014). This study examined whether the color morphs display different levels of aggressive behavior when interacting in a new, unclaimed territory. The results of this study found that color morph did not affect the aggression index (AI), nor most of the other tested aggressive and submissive behaviors, regardless of the morph of the salamander or its testing partner. Although treatment had an overall significant effect on the Lay Next To Other behavior, there was no significant relationship between any two treatments, which may be due to the low sample size of salamanders which displayed this behavior (n=9).

These results initially seem to contradict the findings of Reiter et al. (2014) that striped salamanders are more aggressive, but the variations of the methods used in this study may provide explanation for these differences. Reiter et al. (2014) gave some salamanders time to mark territory (residents), while other salamanders were introduced to those territories (intruders). In this study however, both salamanders were introduced at the same time. This could suggest that both morphs initially display the same degree of aggressive behavior, and do not begin to differ until a territory has been established. An alternative explanation is that salamanders in different locations have differences in behavior. Quinn and Graves (1999) compared the behaviors of salamanders from Michigan and Virginia, and suggested that Michigan salamanders preferred to settle near other red-backed salamanders, whereas Virginia salamanders avoided conspecifics. It is possible that unknown behavioral differences exist between the Ohio population examined by Reiter et al. (2014) and the southern Virginia population examined here.

When salamanders were collected for behavioral trials, individuals with no other adults under the same board (i.e. either alone or with only juveniles) were preferred for collection; however, if not enough lone adults could be found, adults from cover boards with another adult(s) were collected. This study found that these salamanders collected from boards which had another adult(s) displayed a higher AI than salamanders which were the only adult under their cover board. The presence of one or more adults may incite salamanders to behave more aggressively, and this increased aggression persists against new salamanders in new locations. Furthermore, when taken alongside the findings of Quinn and Graves (1999), this could suggest that the reason Virginia salamanders avoid conspecifics is to avoid aggressive territorial interactions. Additionally, sky conditions were found to have an effect on AI; the “Showers or Light Rain” condition had the lowest mean AI. This could indicate that salamanders are less aggressive in wetter conditions. Mathis (1990) found that salamanders prefer large cover objects with cooler temperatures over small cover objects, and large salamanders would exclude small salamanders from accessing these resources. This study found there was no significant effect of the air or soil temperature the salamander was collected at on AI, but since all salamanders were held and tested at the same temperature, it is possible that temperature does play a role in behavior in the field, particularly in competition over cool areas. However, it may be the case that this significant result was merely a statistical quirk due to a low sample size for some sky conditions, since sky codes of 1 (partly cloudy) and 5 (showers or light rain) had only 7 salamanders collected for each. These inconclusive results indicate that more research on the influences of temperature, moisture, and weather on aggressive behavior is needed.

The results of this study suggest that red-backed salamanders of different populations and regions may display different behaviors. This could be due to climatic differences (e.g.

temperature and precipitation), or differences in population demography. The James River Park salamander population has a much higher population density than any other site studied in the SPARCnet red-backed salamander research network, and mark-recapture studies at other plots within the James River Park frequently find multiple salamanders beneath a single cover board (Hernández-Pacheco et al. 2019). The population density may be so high that it is near impossible for resident salamanders to totally exclude intruders from their claimed territory, which could force salamanders to be more tolerant (i.e. less aggressive) than is usual for the species. Regardless of the precise reasons why populations differ in behavior, future research on red-backed salamander behavior should be aware that their findings may be applicable only to the studied population, and not the species as a whole.

In conclusion, this study found that two color morphs of red-backed salamander from a southern Virginia population display similar levels of aggressive behavior when introduced to a new, unclaimed territory. This is particularly notable because past research with different methods and in a different location found that striped salamanders were more aggressive than lead salamanders (Reiter et al. 2014). Studying these interactions allows us to gain additional knowledge on how study design and geographic region can impact behavioral research. This work can inform efforts to better conserve amphibian populations by demonstrating factors which may increase or decrease aggressive behaviors between individuals.

**Acknowledgements**

I would like to thank the University of Richmond for providing support to the Grayson lab’s salamander research. I would also like to thank Dr. Kristine Grayson for her mentorship and assistance throughout this study and my time performing research in her lab. I would like to thank Hannah Coovert for her aid in developing my research procedures and performing data analysis. I would like to thank Dr. Peter Smallwood for reading over and critiquing this paper. I am also grateful to Dr. Jennifer Sevin for her helpful comments on this paper. Lastly, I would like to thank Bryce Wilk and Nathan Burrell, superintendents of the JRPS, for allowing me to conduct research with the red-backed salamanders in the James River Park. All procedures were approved by the UR Institutional Animal Care and Use Committee (Protocol 16-03-001) and under scientific permits from the Virginia Department of Game and Inland Fisheries (No. 061682).

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**Figures**

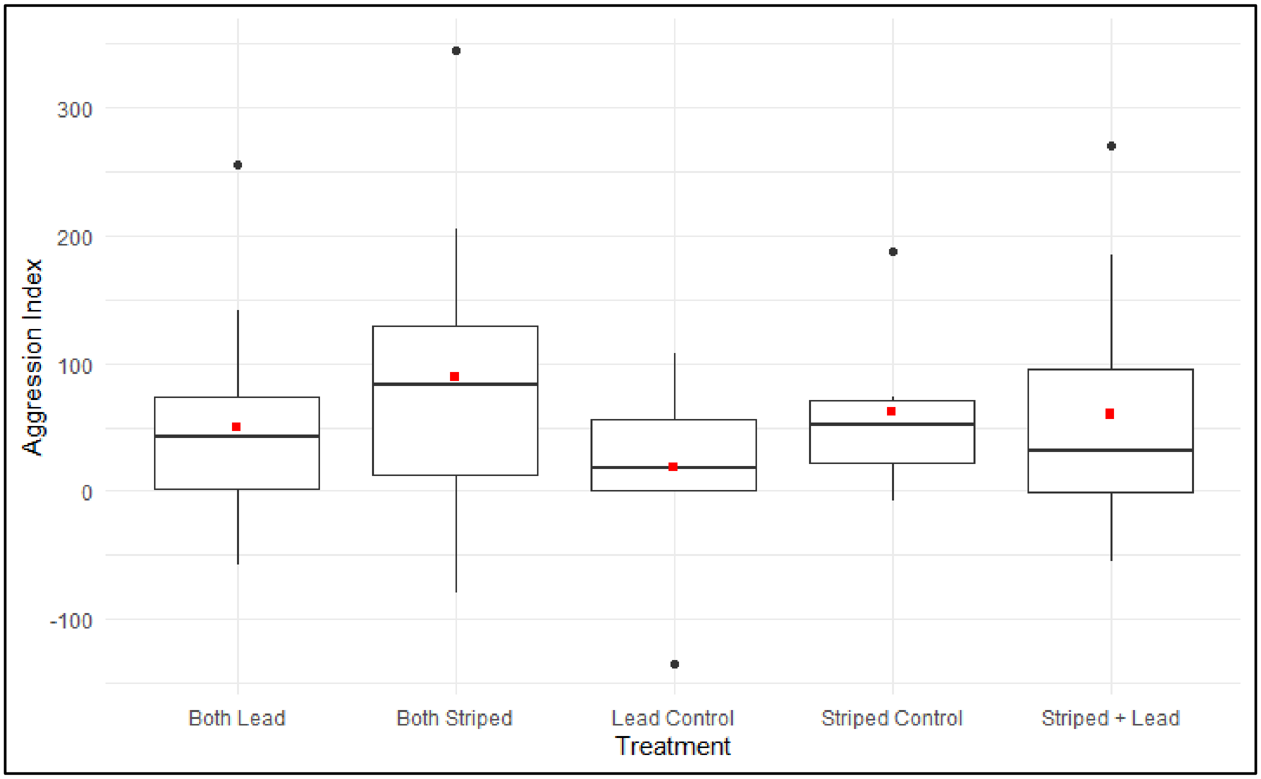


Figure 1. The Effect of Treatment on Aggression Index. Each box indicates the interquartile range, the median is indicated by the middle line, and the mean is indicated by the red square. The top whisker is the greatest point within the range of Q3 + 1.5*IQR, and the bottom whisker is the smallest point within the range of Q1 - 1.5*IQR. Points shown are outliers. There were 18 salamanders in the Both Lead treatment group, 14 salamanders in the Both Striped treatment group, 16 salamanders in the Striped and Lead treatment group, 10 salamanders in the Lead Control treatment group, and 6 salamanders in the Striped Control treatment group.

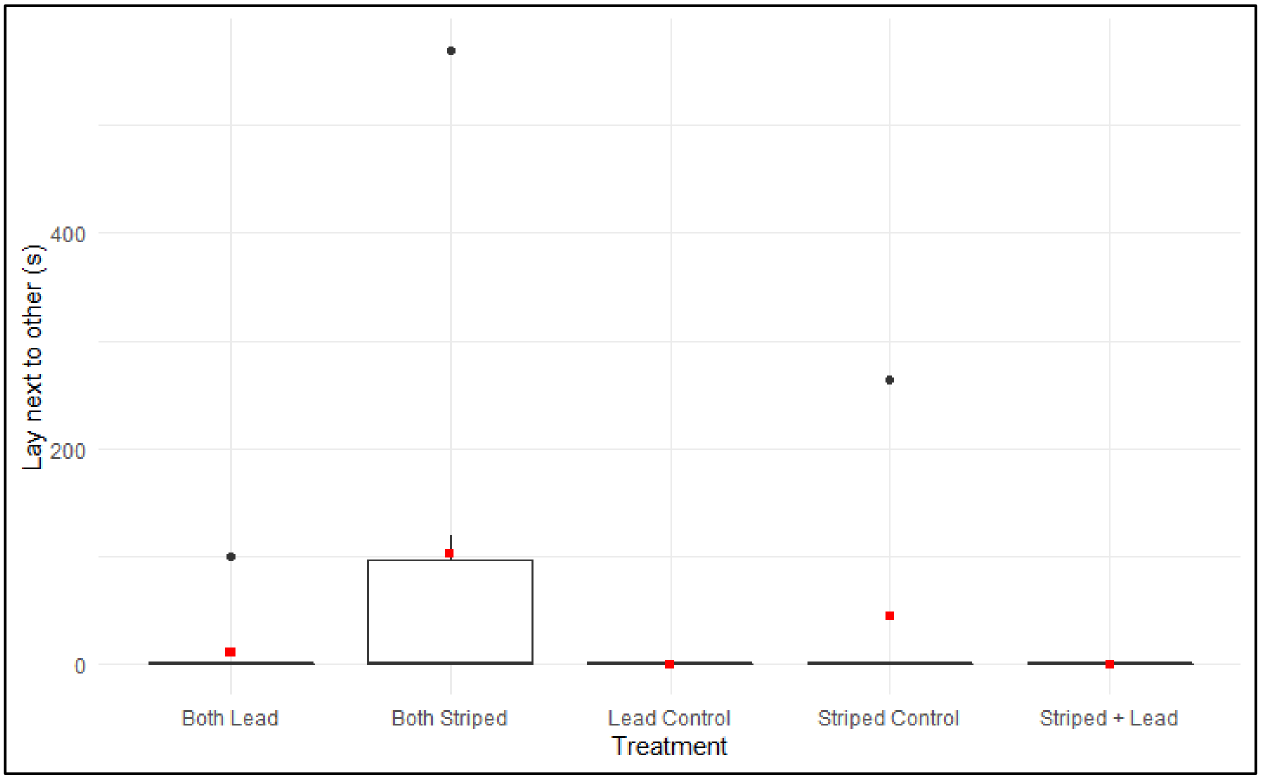


Figure 2. The Effect of Treatment on Duration of the Lay Next To Other Behavior. Each box indicates the interquartile range, the median is indicated by the middle line, and the mean is indicated by the red square. The top whisker is the greatest point within the range of Q3 + 1.5*IQR, and the bottom whisker is the smallest point within the range of Q1 - 1.5*IQR. Points shown are outliers. There were 18 salamanders in the Both Lead treatment group, 14 salamanders in the Both Striped treatment group, 16 salamanders in the Striped and Lead treatment group, 10 salamanders in the Lead Control treatment group, and 6 salamanders in the Striped Control treatment group.

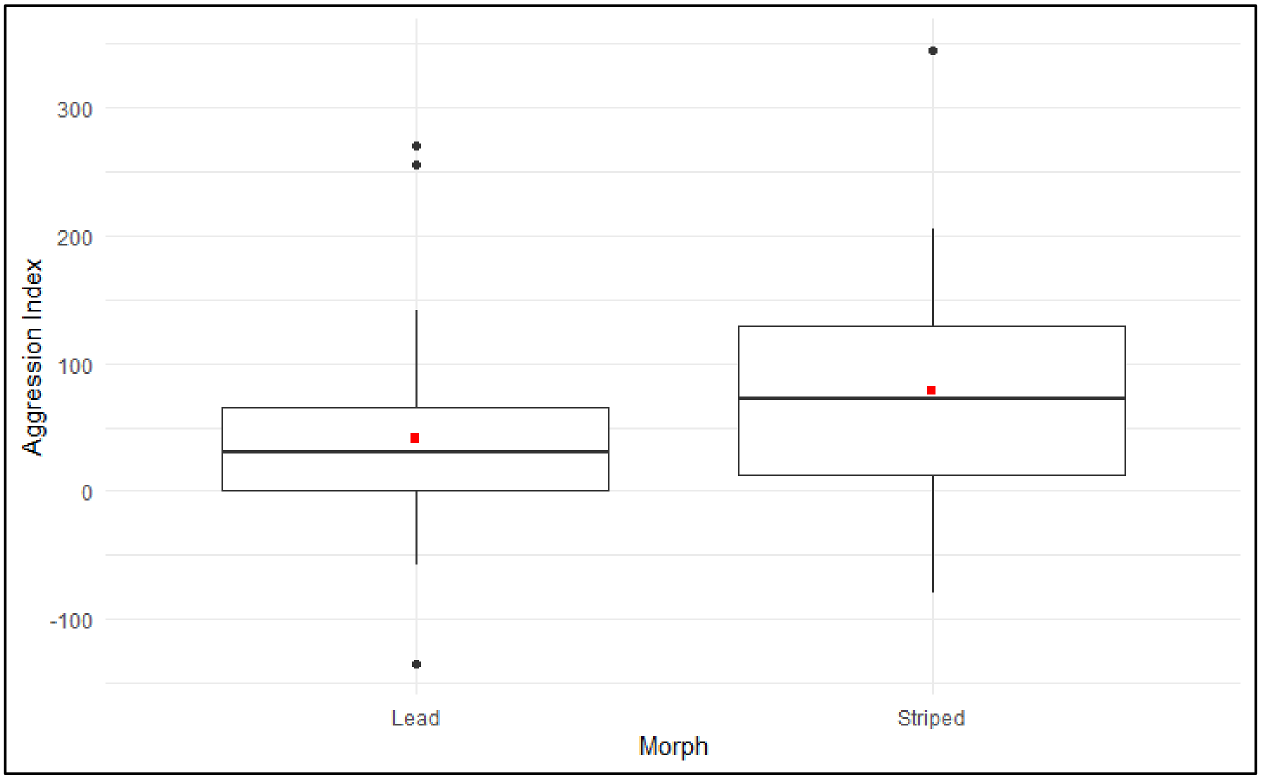


Figure 3. The Effect of Morph on Aggression Index. Each box indicates the interquartile range, the median is indicated by the middle line, and the mean is indicated by the red square. The top whisker is the greatest point within the range of Q3 + 1.5*IQR, and the bottom whisker is the smallest point within the range of Q1 - 1.5*IQR. The points shown are outliers. There were 36 lead salamanders and 28 striped salamanders.

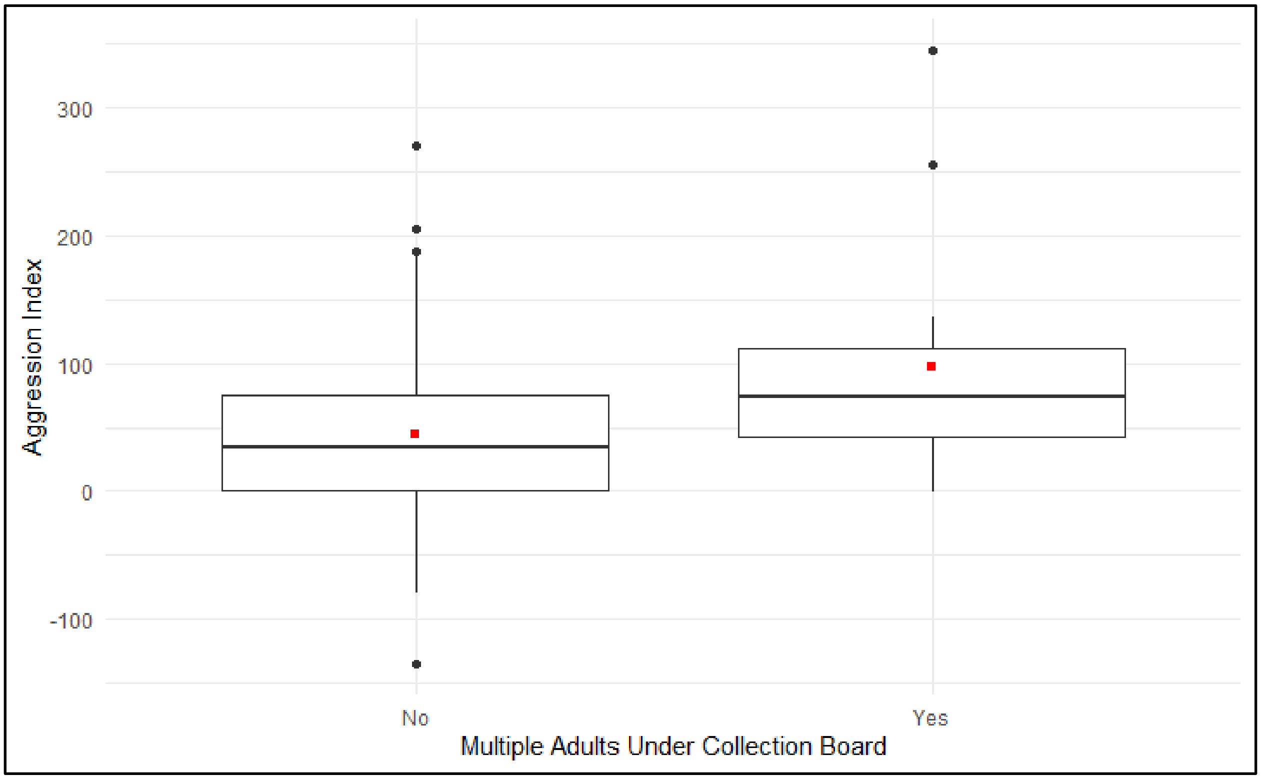


Figure 4. The Effect of the Presence of Multiple Adults Under a Collection Board on Aggression Index. Each box indicates the interquartile range, the median is indicated by the middle line, and the mean is indicated by the red square. The top whisker is the greatest point within the range of Q3 + 1.5*IQR, and the bottom whisker is the smallest point within the range of Q1 - 1.5*IQR. Points shown are outliers. There were 39 salamanders that did not have multiple adults under the collection board, and 15 salamanders that did have multiple adults under the collection board.

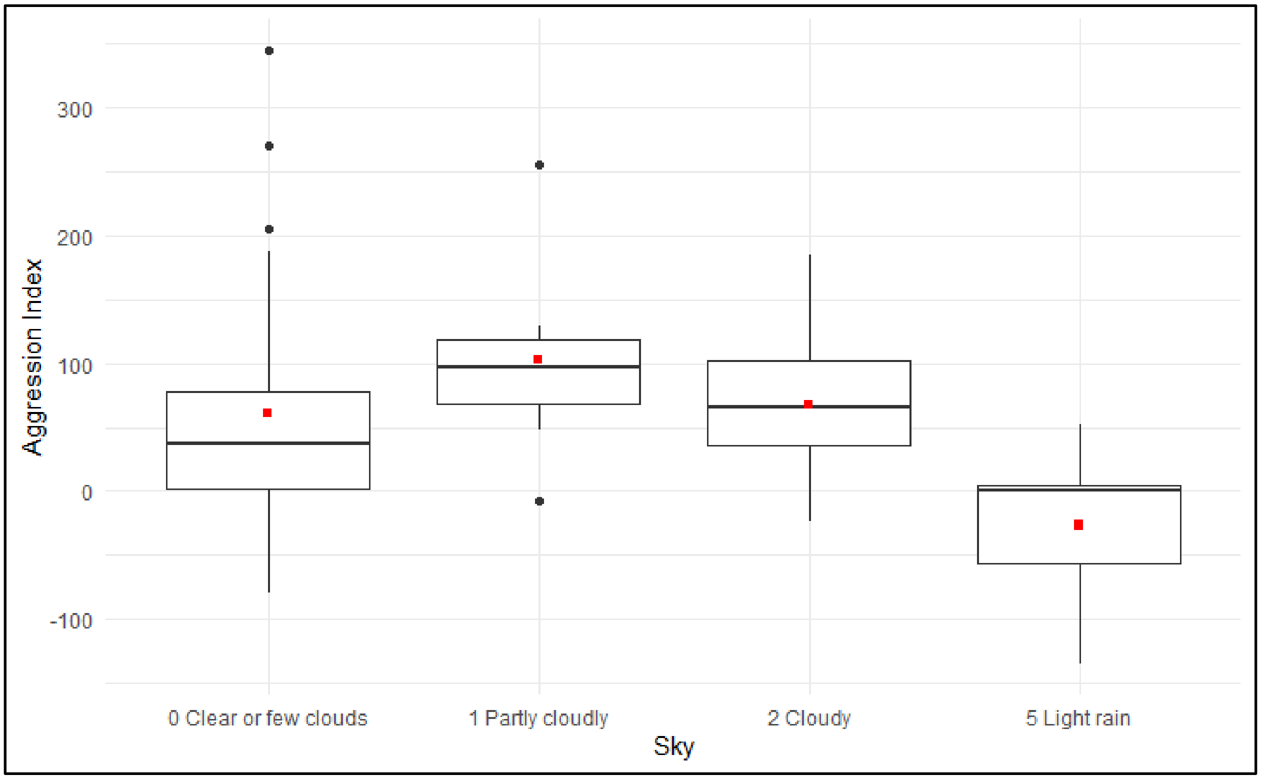


Figure 5. The Effect of Sky Condition on Aggression Index. Each box indicates the interquartile range, the median is indicated by the middle line, and the mean is indicated by the red square. The top whisker is the greatest point within the range of Q3 + 1.5*IQR, and the bottom whisker is the smallest point within the range of Q1 - 1.5*IQR. The points shown are outliers. There were 35 salamanders collected during a sky code of 0, 7 salamanders collected during a sky code of 1, 15 salamanders collected during a sky code of 2, and 7 salamanders collected during a sky code of 5.

Table 1. Beaufort Scale for measuring wind conditions.

| Beaufort Number | Wind Speed (mph) | Effects on Land |
|---|---|---|
| 0 | <1 | Calm |
| 1 | 1-3 | Smoke drifts, vanes do not move |
| 2 | 4-7 | Wind felt on face, leaves rustle, vanes move |
| 3 | 8-12 | Leaves and small twigs in constant motion |
| 4 | 13-18 | Leaves raised up, small branches move |
| 5 | 19-24 | Small trees sway |
| 6 | 25-31 | Large branches move |
| 7 | 32-38 | Whole trees move |
| 8 | 39-46 | Twigs and small branches break off trees |
| 9 | 47-54 | Slight structural damage |
| 10 | 55-63 | Trees broken, structural damage occurs |
| 11 | 64-72 | Widespread damage |
| 12 | 73 or higher | Destruction |

Table 2. Codes for sky conditions. Adapted from SPARCnet (2015).

| Sky Code | Sky Conditions |
|---|---|
| 0 | Clear or few clouds (<20% of sky) |
| 1 | Partly cloudy or variable (20-50% of sky) |
| 2 | Cloudy or overcast (>50% of sky) |
| 3 | Fog |
| 4 | Mist |
| 5 | Showers or light rain |
| 6 | Heavy rain |
| 7 | Sleet/hail |
| 8 | Snow |

Table 3. Definition of Behaviors. Adapted from Jaeger et al. (2016).

| Behavior | Definition |
|---|---|
| Look Towards | Salamander turns its head to look towards the other |
| Look Away | Salamander turns its head to look away from the other |
| Move Towards | Salamander moves towards the other |
| Move Away | Salamander moves away from the other |
| Raise Trunk | Salamander raises the front of its trunk |
| All Trunk Raised | Salamander raises its entire trunk |
| Walk Around Perimeter | Salamander walks around the perimeter of the container |
| Lay Flat | Salamander lays flat against the bottom of the container |
| Climb Out | Salamander climbs out of the container |
| Lay Next to Other | Salamander lays next to the other |
| Bite | Salamander bites the other |