

**A TOP PREDATOR RETURNS: EFFECTS OF THE EASTERN INDIGO
SNAKE (*DRYMARCHON COUPERI*) ON SNAKE SPECIES IN SOUTHERN
ALABAMA**

An Undergraduate Research Scholars Thesis

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ABSTRACT

A Top Predator Returns: Effects of the Eastern Indigo Snake (*Drymarchon couperi*) on Snake Species in Southern Alabama

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Increasing focus has been placed on snakes and their role in the ecosystem. As a key predator in longleaf pine ecosystems, the eastern indigo snake (*Drymarchon couperi*) feeds on a variety of taxa, but recent studies have shown an innate preference for snakes and pit vipers in particular. Once found throughout the southeastern United States, its decreasing range and numbers resulted in its extirpation from many areas. In 2008, reintroduction efforts for the eastern indigo were initiated in the Conecuh National Forest (CNF) in southern Alabama. Six years after its reintroduction, drift fences were constructed to survey the herpetofauna in control sites as well as sites where the eastern indigo snake was released. The objective of this study was to assess the effects of the eastern indigo snake on snake species in Southern Alabama. Field data were collected from reintroduction and non-reintroduction sites within CNF to test the hypotheses that at reintroduction sites, 1) the capture rates of venomous snakes decreased, 2) the

capture rates of the most common species were reduced, and 3) the average sizes of snakes were larger.

The three most commonly detected snake species were southern black racers (*Coluber constrictor priapus*), eastern copperheads (*Agkistrodon contortrix*), and eastern coachwhips (*Coluber flagellum flagellum*). There were significantly less black racers in the reintroduction sites than the control sites, suggesting the black racer's high numbers and active lifestyle may result in higher predation by the indigo snakes. Surprisingly, the size (total length and mass) of male racers and copperheads and the mass of female coachwhips were significantly smaller in the reintroduction sites. We suggest an relationship between body size and home ranges or daily movements that results in increased predation by indigo snakes. However, difficulties in study design and sample size must be taken into account when interpreting results, and more research is needed to establish direct causal links.

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CHAPTER I

INTRODUCTION

Eastern indigo snakes (*Drymarchon couperi*) are the largest snakes native to North America (Dodd and Barichivich 2007). They are closely associated with the federally threatened gopher tortoise (*Gopherus polyphemus*) and often use tortoise burrows as refuges to escape winter temperatures, leading to the suggestion that gopher tortoise presence may be a limiting factor for the eastern indigo in the northern parts of its range (Hyslop et al. 2009, Stiles 2013). Gopher tortoises and eastern indigos both prefer to live in open-canopy longleaf pine (*Pinus palustris*) ecosystems, which have seen drastic declines of up to 98% over the years as faster-growing pine species such as loblolly pine (*Pinus taeda*) have been planted for timber purposes (Noss et al. 1995, Stiles 2013, McCoy et al. 2013). Frost (1993) estimated the remaining natural longleaf pine forests to be around 3%, with only 3 million of the original 90 million acres remaining in the southeast in the late 1990s (Frost 1993, Longleaf Partnership Council 2014). Increasing development and habitat degradation, as well as the gassing of gopher tortoise burrows during rattlesnake round-ups, led to the decline of the eastern indigo snake and prompted the U.S. Fish and Wildlife Service to list it as federally threatened in 1978 (Greenwalt 1978, Godwin et al. 2011). Although the eastern indigo's historic range extended as far north and west as Alabama and Mississippi, naturally existing populations likely no longer exist in those two states (Enge et al. 2013).

However, the past decade has seen a tremendous rise in longleaf pine restoration efforts across the southeast, including the replanting of longleaf seedlings, removal of invasive vegetation species, and prescribed burning to control dense understory vegetation (Longleaf

Partnership Council 2014). The increasing trend in improved, open-canopy longleaf pine habitat combined with recent legislation outlawing the gassing of gopher tortoise burrows sets an encouraging stage for the eastern indigo snake. Starting in 2010, researchers began reintroducing eastern indigos onto select sites within Conecuh National Forest (CNF) in southern Alabama. A total of 107 snakes were released as of 2015 (Godwin et al. 2011, D.A. Steen, pers. comm.).

Eastern indigos are active foragers and feed on a wide array of animals, including fish, anurans, snakes, turtles, salamanders, invertebrates, birds, and mammals (Mount 1996, Stevenson et al. 2010). Although records illustrate that eastern indigo snakes are generalist predators, snakes are a prominent part of their diet (Stevenson et al. 2010). One study exploring diet preferences in neonate eastern indigos showed they had an innate preference for snakes over house mice (*Mus musculus*) and a preference for copperhead (*Agkistrodon contortrix*) snakes over rat snakes (*Pantherophis spiloides*) (Goetz et al. 2016). Goetz et al. (2016) suggest that pit vipers such as copperheads may play a larger role in eastern indigo diets than previously assumed.

A growing body of literature focuses on snake ecology, highlighting their role as a predator and their impacts on prey populations (Shine and Bonnet 2000, Steen et al. 2014b, Weatherhead and Blouin-Demers 2004). Situations where exotic snakes were introduced and subsequently reduced native wildlife abundance (Burmese python: Dorcas et al. 2012, Sovie et al. 2016, brown treesnake: Savidge 1987, Earl III et al. 2012) clearly illustrate the potential for snakes to dramatically alter prey communities. Steen et al. (2014) identified a negative relationship between the relative abundance of eastern kingsnakes (*Lampropeltis getula*) and the relative abundance of the copperhead—a species commonly preyed upon by kingsnakes-- indicating increases in copperhead populations may result from their release from predation

pressure after widespread kingsnake declines. Guyer et al. (2007) observed this trend in CNF, where eastern kingsnakes have declined significantly and the once-rare copperheads are now one of the most encountered snake species (Graham et al. 2015). The recent reintroduction efforts offer a unique opportunity to explore the effects of the eastern indigo snake on existing herpetofauna in CNF. If eastern indigos have a preference for copperheads in particular like Goetz et al. (2016) suggest, a focused predation on that species may put pressure on their populations. This could have other ecological effects; for example, increased regulation of copperhead populations could allow their interspecific competitors to flourish, leading to increased species evenness and diversity at sites where the eastern indigo is present.

The reintroduction of a predator like the eastern indigo may affect prey communities in a variety of ways, including prey size. An experiment on invasive snake predation of native lizard species found that lizards were larger when snakes were removed, implying more lizards survived or reached a larger size without the predation pressure from the snake (Earl III et al. 2012).

The prevalence of prey individuals in a certain size class may also be influenced by the gape size of the predator. As snakes grow, the size of their mouth (gape) increases, allowing the snake to eat larger prey. Snake species tend to fall into two categories depending on how the lower size limit for prey changes as a function of snake size. Arnold (1993) states that as most snake species grow, both the minimum and maximum prey size increase as the snake drops smaller prey from its diet. In the second category, snakes continue to eat small prey. For example, (Rodríguez-Robles 2002) found that the lower limit of prey mass did not increase with snake mass for the gopher snake (*Pituophis catenifer*). If eastern indigos prey heavily on one size class of snakes, we should expect to see a difference in average size between reintroduction and

control sites. For instance, if the eastern indigos eat larger prey as they grow, we might have more detections of smaller snakes over the years. Although no research has been done on indigo snakes and gape size, records of indigos preying on animals both large and small relative to their body size (Stevenson et al. 2010) support its placement in the second category. If this is the case, there may not be a discernable difference in smaller prey between sites. However, because snakes are limited by gape size (Shine 1991), we might also expect more detections of larger snakes that were over the eastern indigos' maximum prey size. When examining the effect of the Michigan racer (*Coluber constrictor*) on other snakes, Kjoss (2000) found size differences in garter snakes (*Thamnophis sirtalis*) between areas of intensive and limited Michigan racer activity. Racers are known to eat other snakes, and Kjoss (2000) suggested the prevalence of garter snakes >50 cm in areas of intensive racer activity was a result of larger individuals escaping predation. Eastern indigos may have similar effects on prey populations at reintroduction sites in CNF. Of course, this study operates under the assumption that prey populations were similar before and after indigos were introduced, and that any differences that occur are attributable to the eastern indigos' influence.

The objective of this study was to assess the effects of the eastern indigo snake on snake species in southern Alabama by testing the hypotheses that at reintroduction sites, 1) the capture rates of venomous snakes decreased, 2) the capture rates of the most common species were reduced, and 3) the average sizes of snakes were larger. Adding to our knowledge of natural history and interspecific interactions is increasingly important as the eastern indigo becomes the focus of further conservation and reintroduction efforts in the southeastern United States.

CHAPTER II

METHODS

Study Area

This study was conducted in Conecuh National Forest (CNF) in southern Alabama (Figure 1). CNF was established as a National Forest in 1936, and covers a total of 340 km² (Graham et al. 2015). It represents one of the largest areas of longleaf pine forest in Alabama, with the majority of the land consisting of various successional stages of upland longleaf pine managed by the U.S. Forest Service. The remaining land contains mesic flatwood forests, mixed pine-hardwood forest, hardwood forests associated with wetlands and slopes, and agricultural or suburban in-holdings. CNF features several different types of water bodies, including permanent and temporary ponds, bogs, large streams, small whitewater and blackwater streams, swamps, and seepages. Previous studies indicate CNF boasts possibly the highest species richness of herpetofauna in North America north of Mexico, with over 100 species (Graham et al. 2015).

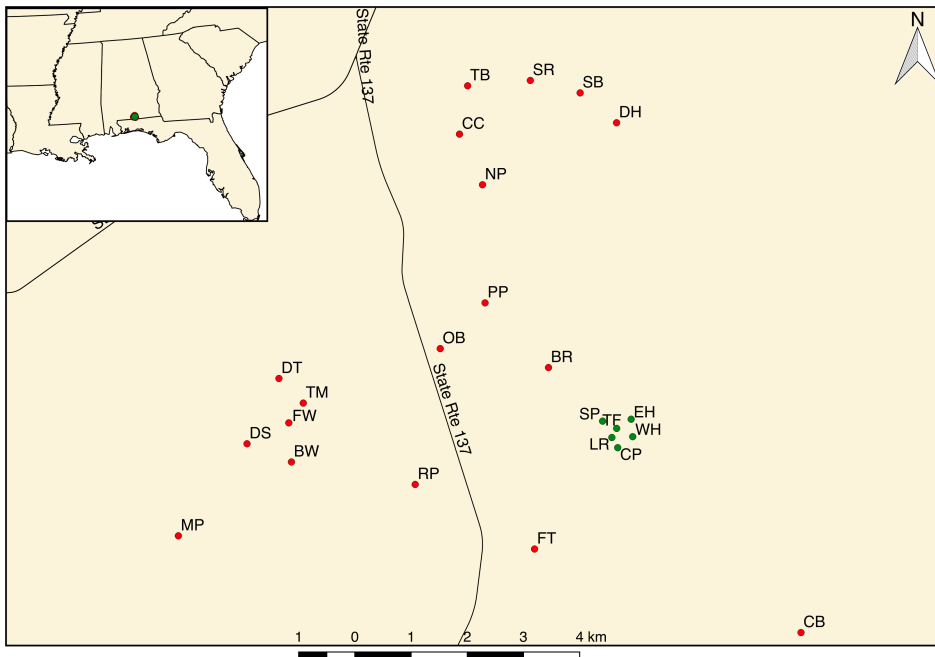


Figure 1: Map of Trap sites in Conecuh National Forest, Alabama. Control sites are red; sites within the indigo reintroduction area are green (SP, EH, WH, LR, CP). Inset: Location of CNF within the southeastern US.

Study Design

Data were collected from a total of 24 drift fence arrays in CNF from April 2015 through July 2016. The 2015 trapping season was from April to October, and included a total of 18 total traps checked daily: 12 control sites and six sites within the reintroduction area. In 2016, six additional control traps were included and all traps were open from March to July. Due to the increased number of trap sites in 2016, half of the traps were checked each day. Control sites consisted of 15 traps outside the 100% minimum convex polygon (MCP) home range of radio-tracked reintroduced snakes and three traps (BR, FT, CB) inside the 100% MCP but well outside the 50% MCP core area (J.A. Stiles, pers. comm.). All six reintroduction sites are within the 50% MCP core area.

Each trap site had one drift fence array consisting of four 30 m mesh hardware cloth fences extending from a box trap with four funnel entrances (adapted from Burgdorf et al. (2005)). Any snakes caught in the trap were sexed with a probe, weighed, measured (snout-to-vent [SVL] length and tail length) with a measuring tape, and given a unique cautery mark (Winne et al. 2006). All snake species except black racers (*C. constrictor*) and copperheads (*A. contortrix*) were given a Passive Integrated Transponder (PIT) tag to enable identification of recaptured individuals.

Although the number of captures may not reflect the true relative abundance due to variations in detection probabilities, the low density and cryptic nature of many large snakes

makes true abundance difficult to measure and detection probabilities often inapplicable (Anderson 2001, Steen 2010, Steen et al. 2012a). As the best method currently available to us, we rely on the assumption that our sampling effort was sufficient to allow the number of captures to provide some indication of abundance. Due to differences in trapping effort (varying numbers of traps and trap days) between the control sites and reintroduction sites, we calculated catch per unit effort (CPUE) by dividing the number of captures by the total number of trap days in each trapping season. One trap day refers to one 24-hour period in which a trap is open. Total CPUE refers to the total number of captures divided by the number of trap days combined from the 2015 and 2016 seasons. We assumed these capture rates correlated with relative abundance (i.e., higher capture rates reflect higher abundance) and conduct our analyses using CPUE rather than raw detection counts (Rodda 2012).

To address the first hypothesis, we performed two-sample t-tests (assuming unequal variance) to determine if there were any statistical differences in the CPUE of venomous snakes between control sites and reintroduction sites by grouping all the pit vipers together. Species in the pit viper category included copperheads, cottonmouths (*A. piscivorus*), eastern diamond-backed rattlesnakes (*Crotalus adamanteus*), timber rattlesnakes (*C. horridus*), and pygmy rattlesnakes (*Sistrurus miliarius*). We also examined the CPUE for all snake species combined, as well as all snake species excluding pit vipers. Each t-test compared the CPUE of control sites to the CPUE of reintroduction sites. For each analysis, three separate t-tests were conducted using the 2015 data, 2016 data, and the total CPUE from both years. Recaptured snakes were not counted more than once in the analyses; only the most recent record of an individual was used. . For each analysis, three t-tests were conducted using 2015 data, 2016 data, and the total CPUE. Recaptured snakes were not counted more than once in analyses; only the most recent record of

an individual was used. For the second hypothesis, we used t-tests to test for differences in CPUE of the three most commonly caught species (southern black racers, copperheads, and eastern coachwhips) in control sites and reintroduction sites. The third hypothesis was evaluated by testing for statistically significant differences in mass or total length of snakes between sites in the control and reintroduction areas. To minimize the potential effects of sexually dimorphic size differences, males and females of each species were analyzed separately. A species accumulation curve was plotted and species richness was determined for both reintroduction and control sites. Abundant species were expected to be important in our analyses, so Simpson's Diversity Index was used to calculate the dominance ($D = \sum n(n - 1)/N(N - 1)$) and evenness ($1 - D$). Additionally, because habitat affects species distribution and has been shown to influence the strength of interspecific interactions on species co-occurrence (Steen et al. 2012b, Steen et al. 2014a), land coverage for all of the trap sites were categorized using Alabama Gap Analysis Project (GAP) shapefiles in QGIS.

CHAPTER III

RESULTS

We caught a total of 17 snake species, with 405 recorded captures over 4845 total trap days. After removing extra records from recaptured snakes, there were a total of 386 individuals. The three most commonly caught species were black racers ($n = 127$), copperheads ($n = 106$) and coachwhips ($n = 38$). See [Table 1](#) (Appendix A) for the total number captures and CPUE for all species and [Figure 12](#) for species accumulation curves (Appendix B). From the 18 traps in the control area, we caught 297 snakes over 3417 trap days (0.0869 snakes/trap day). The most commonly captured species was the black racer ($n = 106$), followed by copperheads ($n = 77$) and coachwhips ($n = 27$). The six traps in the reintroduction area captured 89 snakes in 1428 trap days (0.0623 snakes/trap day). Copperheads were most common ($n = 29$), followed by racers ($n = 21$) and coachwhips ($n = 11$). In the control area, the species richness was 16 and the Simpson Diversity evenness ($1 - D$) was 0.79. The reintroduction area had a species richness of 10 and a Simpson Diversity evenness of 0.81.

Hypothesis 1: Capture Rates of Venomous Snakes

When pit vipers were grouped in a category there was no significant difference found in 2015 ($df = 8$, $p = 0.83$), 2016 ($df = 22$, $p = 0.055$), or total CPUE ($df = 10$, $p = 0.51$), although the average capture rates for 2016 approached significance with reintroduction sites having 0.015 less snakes/trap day than control sites ([Figure 2](#), Appendix B). Copperheads and eastern diamond-backed rattlesnakes were examined at the species level; copperheads are discussed in

the next section (Figures 3 and 4, Appendix B). There was no significant difference in the total capture rates of the diamond-backed rattlesnakes (df = 21, p = 0.17).

There was also no significant difference in CPUE for non-pit viper snakes in 2015, 2016, or total (df = 22, p = 0.09). The CPUE for all snake species was smaller in the reintroduction sites for both 2015 and 2016, but the difference was only significant in 2016 where the average CPUE in the reintroduction sites was 0.891 snakes/trap day less than the control sites (df = 21, p = 0.03) (Figure 5, Appendix B).

Table 2: Tests for Significant Differences in Capture Rates of Pit Vipers Between Reintroduction and Control Sites (alpha = 0.05; *significant at p = <0.05, ** significant at p = <0.01, *** significant at = <0.0001)

Group	2015	2016	Total
Venomous (pit vipers)	df = 8, p= 0.83	df = 22, p = 0.055	df = 10, p = 0.51
Copperheads	df = 8, p= 0.83	df = 22, p = 0.055	df = 10, p = 0.51
Eastern diamond-backed rattlesnakes	df = 16, p = 0.27	df = 13, p = 0.45	df = 21, p = 0.17
Non-pit vipers	df = 16, p = 0.91	df = 19, p = 0.07,	df = 22, p = 0.09
All snake species	df = 16, p = 0.79	df = 21, p = 0.03*	df = 22, p = 0.057

Hypothesis 2: Capture Rates of the Three Most Common Species

Although the total CPUE (2015 and 2016) was less in the reintroduction area than the control area for all three of the most common species, the difference was only significant for racers (df = 21, p = 0.012) (Figure 6, Appendix B). The average CPUE for racers was 0.038 snakes/trap day in the control sites and 0.015 snakes/trap day in the reintroduction sites. There were no obvious differences in captures rates of coachwhips (Figure 7, Appendix B).

Table 3: Tests for Significant Differences in Capture Rates of the Three Most Common Species Between Reintroduction and Control Sites (alpha = 0.05; *significant at $p < 0.05$, ** significant at $p < 0.01$, *** significant at $p < 0.0001$)

Species	2015		2016		Total	
Black racer	$p = 0.26$	$df = 16$	$p = 0.016^*$	$df = 21$	$p = 0.012^*$	$df = 21$
Copperhead	$p = 0.85$	$df = 8$	$p = 0.14$	$df = 21$	$p = 0.78$	$df = 10$
Coachwhip	$p = 0.79$	$df = 9$	$p = 0.91$	$df = 8$	$p = 0.94$	$df = 9$

Hypothesis 3: Snake Sizes

Surprisingly, male racers and copperheads were significantly shorter ($df = 9$, $p = 0.04$; $df = 48$, $p = 0.002$) and weighed less ($df = 11$, $p = 0.016$; $df = 51$, $p = 0.0003$) in the reintroduction sites (Table 4, Appendix A). The average length of male copperheads in the reintroduction sites was 130.0 mm shorter and the average mass of males was 65.5 g less than that of males in control sites. Male racers were on average 168.9 mm shorter and 56.1 g lighter in the reintroduction sites. The average length of male coachwhips was 76.5 mm shorter and the average mass was 81.7 g less in the reintroduction sites, but the difference wasn't significant ($df = 4$, $p = 0.76$; $df = 7$, $p = 0.58$) (Figures 8 and 9, Appendix B). Interestingly, although the mass of coachwhip females was significantly smaller in the reintroduction sites ($df = 15$, $p = 0.03$), female racers and copperheads showed no difference (Figures 10 and 11, Appendix B). Female coachwhips weighed an average of 202.9 g less in the reintroduction sites, and although the difference wasn't statistically significant, they were 316.6 mm shorter on average ($df = 7$, $p = 0.09$). Because each of the three species had one sex that showed smaller sizes in the reintroduction sites, capture rates for both sexes were compared. Analyses also showed capture rates of male racers were lower than those of females in reintroduction sites in the 2016 and Total tests ($df = 19$, $p = 0.01$; $df = 21$, $p = 0.018$), but this trend did not hold true for male copperheads or female coachwhips.

CHAPTER IV

DISCUSSION

Overall species richness was higher for the control sites (=16) than reintroduction sites (=10), but this difference is more likely due to larger sampling effort in control sites than any effect caused by indigo snakes. While species accumulation curves produced for both areas were similar in the beginning, the curves show our samples approaching the asymptote for the control sites but not reintroduction sites, indicating sampling effort may not have been great enough in the reintroduction sites to fully estimate the species richness ([Figure 12](#), Appendix B). Because species richness depends on sample size when combined across habitats due to changes in species composition, the wider geographic range and variety of habitats covered by the control sites in comparison to the more clustered reintroduction sites may also affect the observed species richness (Colwell et al. 2004). Graham et al. (2015) documents a total of 36 snake species found in CNF, but many of those species are rare, extirpated, or with life history strategies our traps weren't designed to capture (i.e., arboreal, aquatic, or semi-fossorial). Although the Simpson's Indices values are not directly comparable between the control and reintroduction areas due to differences in habitat and the number of sites, we interpreted these values (control: 0.79; reintroduction: 0.81) independently to mean that both areas had reasonably high diversities and evenness.

Hypothesis 1: Pit Vipers

We observed smaller capture rates for pit vipers in sites where indigos were reintroduced in all three tests, but the differences weren't significant (although they approached significance

in 2016). Grouping multiple pit viper species into one category may have obscured species-specific trends, but the relatively low capture rates of pit vipers prevented analysis for many venomous snakes (excluding copperheads) at the species level. Although detected substantially less in comparison to copperheads, the pit viper species with the next highest capture rate was the eastern diamond-backed rattlesnake. The lack of significant difference in capture rates between control and reintroduction areas may imply indigo snakes are not significantly affecting rattlesnake populations, but it could also mean our sampling effort was not high enough to overcome the low densities and detectability of this species sufficiently to observe any differences.

Hypothesis 2: Common Species

Contrary to our expectations of copperheads as an important prey species of the indigo snake, the relative abundance of copperheads was not significantly less in the reintroduction sites. The visible differences in capture rates of black racers but not copperheads or coachwhips could be explained by a combination of three factors: 1.) relative abundance, 2.) foraging and antipredator behavior, and 3.) home range size.

Black racers had the highest overall capture rates of any species in our study—they are categorized as an abundant species in CNF by Graham et al. (2015) and represented the most frequently caught snake species in drift fences within CNF and the adjacent Solon Dixon Forestry and Education Center from 2002-2006. Similar to eastern indigo snakes, black racers are active, diurnal foragers with high rates of daily movements (Plummer and Congdon 1994). The eastern indigo snakes may be taking advantage of the racers' high relative abundance and movements and preying on them more than copperheads or coachwhips. Furthermore, Saviola

et al. (2011) conducted laboratory tests during which adult indigos responded with increased tongue flicks significantly more to visual cues of prey (rather than just chemicals cues or a combination of both), suggesting visual stimuli such as movement are important in initiating their predation response. Despite Saviola et al.'s results which emphasize the importance of visual cues, Goetz et al. (2016) showed neonate indigos gave increased tongue flicks when exposed to copperhead scent versus rat snakes or mice. However, these results are not necessarily contradictory because of differences in study design. Saviola et al.'s experiment took place with the snakes in Plexiglass boxes with live mice on the other side of either solid or perforated walls. Because Goetz et al. used Q-tips containing prey scent the indigo snakes may have already been stimulated by the movement of the Q- tip to initiate tongue flicks, and then showed differences in responses according to their diet preference. Saviola et al. (2011) point out that indigo snakes may become more receptive to chemical cues once visual cues cause them to initiate tongue flicks. If indigo snakes are attracted by movement and adult racers respond to predator presence by fleeing (Creer 2005, Jackson et al. 1976), indigos may be more likely to detect racers and initiate predation via visual cues rather than copperheads that rely heavily on cryptic behavior to avoid detection by predators (Jackson et al. 1976). Wide-ranging foragers or mobile species such as black racers often experience higher predation risk than sit-and-wait ambush predators like pit vipers (Secor 1995, Bonnet et al. 1999), so it makes sense that black racers would be predated upon more by indigo snakes.

Home range size could be a factor affecting prey interception by indigos, because species with home ranges under a certain area are more likely to occur entirely within the reintroduced indigos' 50% MCP home range. Because of the increased eastern indigo activity and an assumed higher density of indigos within that area, prey species would be more likely to encounter an

indigo snake. For example, average home range sizes (100% MCP) in the literature ranged from 11.45 ha to 25.3 ha for racers (Carfagno and Weatherhead 2008, Klug et al. 2011) and from 1.83 ha to 17.49 ha for copperheads (Smith et al. 2009, Carter 2012). In contrast to copperheads and racers, coachwhips tend to have much greater ranges: studies document average home ranges from 53.4 ha to 177 ha, with several accounts of ranges over 100 ha (Secor 1995, Howze and Smith 2015, Halstead et al. 2009, Dodd and Barichivich 2007). Perhaps coachwhips, with their larger home ranges and high dispersal distances, overlap less with the reintroduction area than racers and copperheads and are spending less time in areas of high indigo activity, thus reducing their risk of predation.

Hypothesis 3: Body Size

We did find differences in body size between the reintroduction and control areas, but instead of finding larger snakes in reintroduction sites like we hypothesized, they were smaller. Upon further consideration, the flaws in our hypothesis are easy to spot. The eastern indigo snake is the largest native non-venomous snake in North America and is capable of eating prey almost as large as itself (Dodd and Barichivich 2007, Stevenson et al. 2010). The original thinking was the young head-started indigos that were reintroduced would be relatively small and therefore be limited by gape-size when it came to preying on the larger snakes. However, because the young indigo snakes were raised in captivity and fed regularly for two years they were already 1181 mm – 1540 mm long when released (Godwin et al. 2011), making them more than capable of preying on medium to large sized snakes. Stevenson et al. (2010) provide prey records documenting indigo snakes in the same size class as the reintroduced snakes preying on snakes over 1000 mm in length. For example, a 1524 mm indigo ate a 1168 mm racer. Because

the first cohort was released in 2010, indigo snakes in CNF have had 5-6 years to grow before our data was collected, making it exceedingly unlikely that gape-limitations would affect their prey choice.

One potential explanation for the smaller average body size between sexes in the reintroduction zone is that the larger sex has a larger home range and/or higher daily movements, increasing the likelihood of interception by predators such as indigo snakes. Previous studies have highlighted the link between movement and mortality: larger male snakes are at greater risk of mortality from predation or anthropogenic causes, as are mobile species that have higher dispersal rates (Bonnet et al. 1999, Bonnet and Naulleau 1996). Because of mate-seeking behaviors that result in increased movement during the reproductive season, adult males may experience more exposure to mortality than females (Aldridge and Brown 1995).

This explanation would seem to fit quite well for copperheads, in which males grow larger than females, have larger home ranges, and are more active than females (Smith et al. 2009, Sutton et al. 2017, Carter 2012). Greater activity and movement for males within the reintroduction area where indigo snakes are clustered would increase the likelihood of predation. For racers and coachwhips—species where the female is the larger sex—this explanation requires a little bit more stretching but is still quite possible. Among racers, males may be more active and have greater daily movements than females (Carfagno and Weatherhead 2008), which would put them at increased risk of predation. Our findings of significantly fewer male racers in reintroduction zones lend support to this idea. However, reports of the influence of sex on home range size in racers are conflicted, with some indicating males have larger home ranges (Klug et al. 2011) and others found no significant difference in home ranges between sexes (Carfagno and Weatherhead 2008). The literature on coachwhips was similarly conflicted; studies documented

no difference in home range size between the sexes (Johnson et al. 2007, Halstead et al. 2009) as well as males having larger overall ranges but similar core ranges as females (Howze and Smith 2015). If female coachwhips were more active or moved farther distances than males, the smaller size of female coachwhips in the reintroduction zone would fit our explanation, but Howze and Smith (2015) and Johnson et al. (2007) report similar or no significant difference in movements between sexes. Females of some species exhibit increased dispersal or movement during the reproductive season related to oviposition and experience higher predation risk as a result (Bonnet et al. 1999, Macartney et al. 1988); it's possible that female coachwhips are one such species. If there is a threshold of home range size that affects the probability of overlap with indigos as suggested in the previous section, another explanation may be that male coachwhips with significantly larger home ranges are more likely to occur away from areas of high indigo activity and escape predation slightly more than females.

Our explanation relies on the assumption that body size is correlated with distance moved and/or home range, to which there are many contradictory reports (Macartney et al. 1988, Halstead et al. 2009, Johnson et al. 2007). The literature indicates this may be species-specific (Bonnet et al. 1999), with no relationship between body size and movement or home range for racers (Plummer and Congdon 1994), but positive correlations or conflicting reports for coachwhips (Johnson et al. 2007, Halstead et al. 2009, Hyslop et al. 2009). Mitrovich et al. (2009) found differences in size-specific movements depending on study site; larger coachwhips had larger home ranges in smaller, more crowded study sites but smaller snakes had the biggest home ranges in a large study site (which they attribute to the foraging behavior of younger snakes).

Macartney et al. (1988) conducted a review of factors affecting home range and movement patterns in snakes and emphasized there is extreme variation within species to the point where there may not be a characteristic pattern for any species—especially those with wide geographic ranges such as our three target species. Several factors have been implicated as predictors of movement and range, including sex, size, prey availability, habitat quality, availability of refugia for thermoregulation and predator avoidance, reproductive behaviors (mate-seeking or oviposition), and migratory behaviors (Macartney et al. 1988, Carter 2012, Hyslop et al. 2014, Hyslop et al. 2009, Kapfer et al. 2010, Halstead et al. 2009). The wide range of variables influencing the distribution of individuals in space complicates questions related to movement patterns in snakes, and untangling the influence of these variables can be very difficult. Additionally, studies illustrating differences among populations of the same species imply that home ranges may change according to site-specific factors such as habitat configuration, population density, resource availability, trophic-level/diet, or temporal responses to environmental conditions like drought (Plummer and Congdon 1994, Mitrovich et al. 2009). Consequently, generalizing from studies performed in other geographic locations—even within the same species—may not be meaningful. The addition of information on movement patterns of racers, copperheads, and coachwhips in relation to eastern indigo snakes in Conecuh National Forest could provide much-needed clarity to the patterns we observed in this project.

Assumptions

As previously discussed, this study relies on several major assumptions that must be taken into consideration: 1) our capture rates give an accurate indication of relative abundances of the species we are analyzing; 3) habitat isn't exerting a major influence on the capture rates of

our target species; 2) indigo snakes have remained largely within the original area they were first reintroduced.

Our use of CPUE rather than raw capture counts helps control for differences in trapping effort, allowing us to interpret capture rates as an index of actual abundance. According to intense previous surveying efforts and reports of relative abundances from CNF (Graham et al. 2015), we successfully detected five of the six “abundant” species, seven of the 10 “common” species, three of the six “uncommon” species, and two of the 13 “rare” species. Moreover, our 2015 - 2016 data seem to reflect the previously higher captures rates for racers, copperheads, and coachwhips from drift fences run in 2005 – 2006 (Table 5, Appendix A); in our study, copperheads and racers were both detected within 54 trap days or less in both areas, and coachwhips were detected in 96 trap days or less. Our analyses focused on the three most common species in CNF which are known to be consistently detectable over multiple years. Because of this, we are fairly confident our captures are representative of relative abundance.

Although the potential influence of habitat can't be completely discounted and future research could certainly focus on controlling this variable, black racers and copperheads are both habitat generalists that can take advantage of wide variety of ecosystems. Because they are found in abundance throughout CNF Graham et al. (2015), we don't expect them to vary dramatically between habitats in our study area. Likewise, although the indigo snake is known for its association with longleaf pine uplands, it has a large home range and also makes use of pine flatwoods, swamps, and other lowland habitats (Stevenson et al. 2010, Stiles 2013, Hyslop 2007). Coachwhips, although abundant, are encountered less and are usually in upland habitats like open, xeric longleaf pine stands (Graham et al. 2015). In our study, the proportions of sites in each land cover was roughly similar for both areas and the majority of sites in both our control

area and reintroduction area contained upland pine forests (Table 6, Appendix A). Other land cover included southern mesic slope forest, successional shrub/scrub, and developed open space.

Radio-telemetry data from the original 38 indigo snakes reintroduced in 2010 and 2011 (1445 locations) were used to create a 100% MCP home range for all the released snakes (Godwin et al. 2011). The 100% MCP covered an area of 3,344 ha with the smaller 50% MCP surrounding the six reintroduction sites (J.A. Stiles, pers. comm.). Because indigos have been known to travel distances 5 – 8 km when migrating between winter and summer habitats (Hyslop 2007), it is entirely possible that some individual indigos dispersed outside the bounds of the 100% MCP. The farthest recorded distance from a CNF release site was 5.94 km with the average for all the snakes being 1.57 km (Godwin et al. 2011). It is also possible that indigos were present around the control traps that are within the total 100% MCP (BR, FT, CB). However, since the majority of activity was clustered within the 50% MCP around the reintroduction area, that is where we expect indigos to exert observable predation pressure on other snake species.

CHAPTER V

CONCLUSION

In summary, we discovered several interesting patterns in snake species that eastern indigos are known to prey upon. The lower relative abundances of black racers (indicated by significantly smaller capture rates) in reintroduction sites suggest indigo snakes may be taking advantage of black racers as a food source. The trend of smaller sizes in one sex captured in reintroduction area in all three species is intriguing and warrants further consideration, and we suggest it may be related to home range size and/or daily movement. Research on species-specific movement and spatial ecology data from populations within CNF would be helpful in illuminating the interspecific interactions that could be occurring. Our results imply the reintroduced indigo snakes may indeed be impacting other snake species in CNF, but the mechanism for these differences is unclear and our current data is insufficient to establish direct casual links. More analyses could be conducted to examine habitat as a potential influencing factor as well as account for the greater trapping effort from the six control sites added in 2016, which possibly affected the significance of our results. In addition, Graham et al. (2015) provide capture rates and sizes (although not distinguished by sex) for black racers, copperheads, and coachwhips from CNF in 2005-2006, and additional analyses could compare these rates and size-frequencies for our species before and after the reintroduction.

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APPENDIX A – TABLES

Table 1: Catch Per Unit Effort (CPUE) and Total Number of Snakes Caught by Species in Control and Reintroduction Areas

	Species	Total caught	Total CPUE	Control Area (18 sites)	Control CPUE	Reintroduction Area (6 sites)	Reintroduction CPUE
1	<i>Coluber constrictor</i>	127	0.0262	106	0.0310	21	0.0147
2	<i>Agkistrodon contortrix</i>	106	0.0219	77	0.0225	29	0.0203
3	<i>Coluber flagellum</i>	38	0.0078	27	0.0079	11	0.0077
4	<i>Pantherophis guttatus</i>	23	0.0047	13	0.0038	10	0.0070
5	<i>Pantherophis spiloides</i>	20	0.0041	20	0.0059	0	0.0000
6	<i>Crotalus adamanteus</i>	18	0.0037	15	0.0044	3	0.0021
7	<i>Pituophis melanoleucus</i>	14	0.0029	11	0.0032	3	0.0021
8	<i>Thamnophis sirtalis</i>	12	0.0025	6	0.0018	6	0.0042
9	<i>Heterodon platirhinos</i>	8	0.0017	5	0.0015	3	0.0021
10	<i>Agkistrodon piscivorus</i>	6	0.0012	6	0.0018	0	0.0000
11	<i>Nerodia faciata</i>	5	0.0010	3	0.0009	2	0.0014
12	<i>Sistrurus miliarius</i>	3	0.0006	3	0.0009	0	0.0000
13	<i>Regina rigida</i>	2	0.0004	2	0.0006	0	0.0000
14	<i>Crotalus horridus</i>	1	0.0002	1	0.0003	0	0.0000
15	<i>Farancia abacura</i>	1	0.0002	1	0.0003	0	0.0000
16	<i>Lampropeltis elapsoides</i>	1	0.0002	1	0.0003	0	0.0000
17	<i>Drymarchon couperi</i>	1	0.0002	0	0.0000	1	0.0007
	Total	386	0.0797	297	0.0869	89	0.0623

Table 4: Body Sizes and P-values of Black Racers, Copperheads, and Coachwhips in Control (C) and Reintroduction (R) Areas (alpha = 0.05; *significant at p = <0.05, ** significant at p = <0.01, *** significant at = <0.0001)

Species	Sex	Size measurement	Average (in mm or g)		Results for Total (2015 and 2016 combined)	
Black racer	M	TL	C = 1034.0	R = 865.1	p = 0.04*	df = 9
		Mass	C = 145.7	R = 89.6	p = 0.017*	df = 11
	F	TL	C = 1016.7	R = 1067.8	p = 0.48	df = 15
		Mass	C = 138.9	R = 152.9	p = 0.59	df = 17
Copperhead	M	TL	C = 611.7	R = 481.7	p = 0.002**	df = 48
		Mass	C = 118.7	R = 53.3	p = 0.0003***	df = 51
	F	TL	C = 474.4	R = 460.6	p = 0.76	df = 20
		Mass	C = 64.6	R = 48.3	p = 0.26	df = 30
Coachwhip	M	TL	C = 1684.3	R = 1607.6	p = 0.76	df = 4
		Mass	C = 481.7	R = 400.0	p = 0.58	df = 7
	F	TL	C = 1761.2	R = 1444.6	p = 0.09	df = 7
		Mass	C = 443.7	R = 240.8	p = 0.032*	df = 15

Table 5: Drift fence results from CNF (Graham et al. 2015).

TABLE 2. Results of drift fence surveys within the Conecuh National Forest (CNF) proclamation boundary, 2002-2006. Surveys within the Solon Dixon Forestry and Education Center (SDFEC) were conducted March 2002 – April 2003, and April 2003 – March 2005 (n = approximately 870 trap nights). Surveys within CNF proper were conducted 12 April 2005 – 19 November 2006 (n = 543 trap nights).

species	Dixon Center	Conecuh N.F.	grand total	species	Dixon Center	Conecuh N.F.	grand total
salamanders (8)				lizards (8) <i>ww</i>			
<i>Ambystoma opacum</i>	1	0	1	<i>Plestiodon fasciatus</i>	5	0	5
<i>Ambystoma talpoideum</i>	152	203	355	<i>Plestiodon laticeps</i>	120	59	179
<i>Ambystoma tigrinum</i>	2	0	2	<i>Scincella lateralis</i>	142	14	156
<i>Eurycea chamberlaini</i>	14	0	14	<i>Aspidoscelis sexlineata</i>	117	81	198
<i>Eurycea cirrigera</i>	6	0	6	snakes (25)			
<i>Plethodon grobmani</i>	14	2	16	<i>Cemophora coccinea</i>	7	6	13
<i>Pseudotriton ruber</i>	6	3	9	<i>Coluber constrictor</i>	143	126	269
<i>Notophthalmus viridescens</i>	57	17	74	<i>Coluber flagellum</i>	34	50	84
frogs (18)				<i>Diadophis punctatus</i>	2	1	3
<i>Anaxyrus quercicus</i>	0	7	7	<i>Farancia abacura</i>	4	0	4
<i>Anaxyrus terrestris</i>	3973	485	4458	<i>Heterodon platyrhinos</i>	34	8	42
<i>Acris gryllus</i>	24	101	125	<i>Lampropeltis elapsoides</i>	1	1	2
<i>Hyla chrysoscelis</i>	17	6	23	<i>Nerodia fasciata</i>	3	13	16
<i>Hyla cinerea</i>	5	3	8	<i>Nerodia sipedon</i>	1	0	1
<i>Hyla femoralis</i>	14	51	65	<i>Opheodrys aestivalis</i>	5	1	6
<i>Hyla gratiosa</i>	33	34	67	<i>Pantherophis guttatus</i>	10	9	19
<i>Hyla squirella</i>	6	7	13	<i>Pantherophis spiloides</i>	15	22	37
<i>Pseudacris crucifer</i>	16	1	17	<i>Pituophis melanoleucus</i>	13	23	36
<i>Pseudacris ornata</i>	5	0	5	<i>Regina rigida</i>	0	2	2
<i>Pseudacris nigrita</i>	1	5	6	<i>Storeria occipitomaculata</i>	7	11	18
<i>Lithobates capito</i>	0	78	78	<i>Tantilla coronata</i>	68	5	73
<i>Lithobates catesbeianus</i>	49	53	102	<i>Thamnophis sauritus</i>	0	2	2
<i>Lithobates clamitans</i>	486	262	748	<i>Thamnophis sirtalis</i>	14	35	49
<i>Lithobates grylio</i>	0	5	5	<i>Virginia striatula</i>	0	5	5
<i>Lithobates sphenoccephalus</i>	287	432	719	<i>Virginia valeriae</i>	1	1	2
<i>Scaphiopus holbrookii</i>	1573	275	1848	<i>Agkistrodon contortrix</i>	41	154	195
<i>Gastrophryne carolina</i>	3696	45	3741	<i>Agkistrodon piscivorus</i>	5	6	11
turtles (8)				<i>Crotalus adamanteus</i>	11	22	33
<i>Chelydra serpentina</i>	1	0	1	<i>Crotalus horridus</i>	6	0	6
<i>Deirochelys reticularia</i>	2	1	3	<i>Sistrurus miliarius</i>	5	11	16

Table 6: Number and Proportion of Sites with Associated Land Cover in Control and Reintroduction Sites (As Categorized by the Alabama Gap Analysis Project (GAP))

Landcover	Control Sites		Reintroduction Sites	
	# of sites	Proportion of sites	# of sites	Proportion of sites
Upland Longleaf Pine Woodland; Loblolly woodland	6	0.33	3	0.50
Upland Longleaf Pine Woodland	9	0.50	1	0.17
Southern Mesic slope forest	2	0.11	1	0.17
Successional Shrub/scrub (clear cut)	1	0.06	0	0.00
Developed open space	0	0.00	1	0.17

APPENDIX B – FIGURES

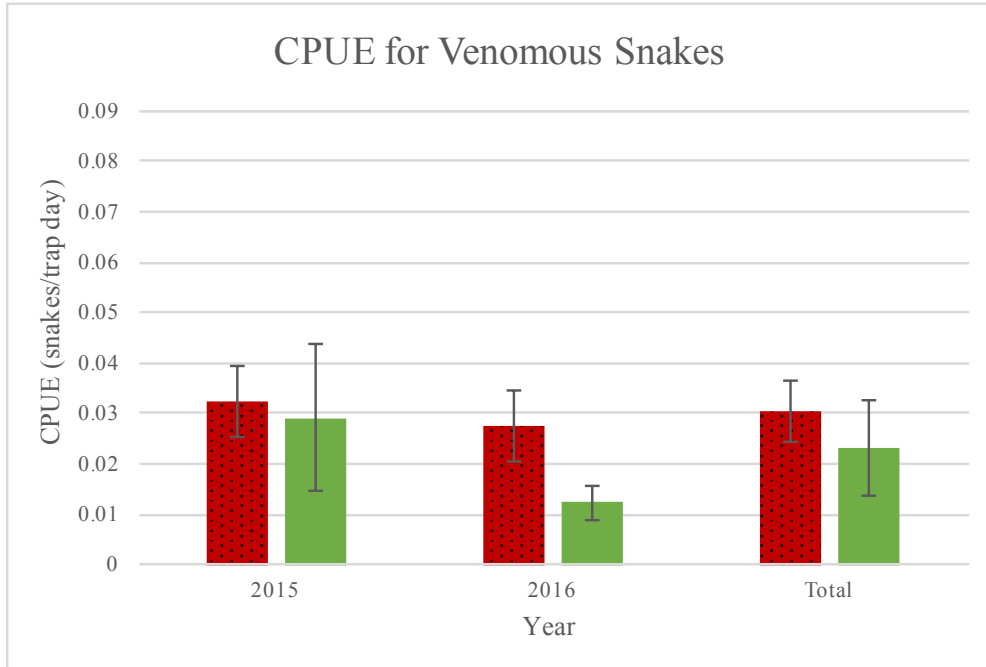


Figure 2: Average Capture Rates for Pit Vipers Species in Control and Reintroduction Sites

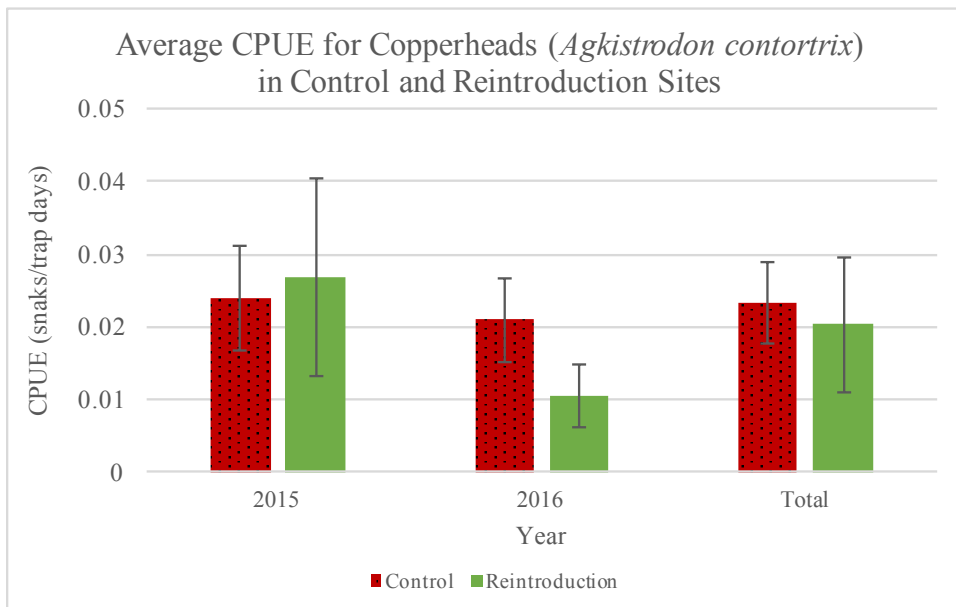


Figure 3: Average Capture Rates for Copperheads (*Agkistrodon contortrix*) in Control and Reintroduction Sites

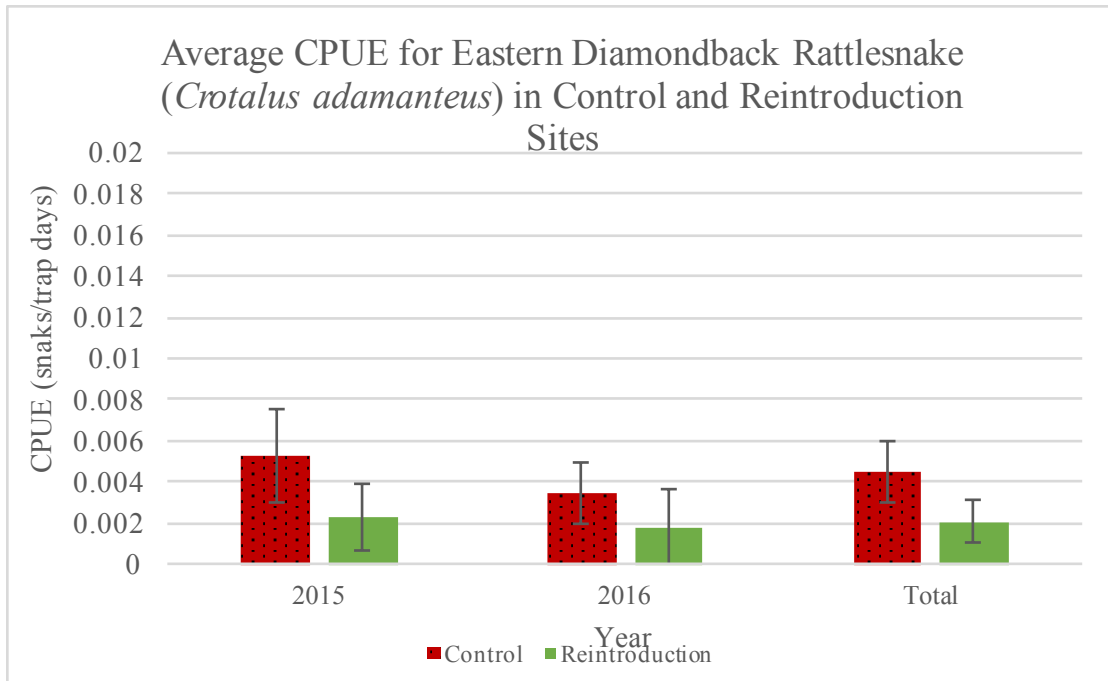


Figure 4: Average Capture Rates for Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*) in Control and Reintroduction Sites

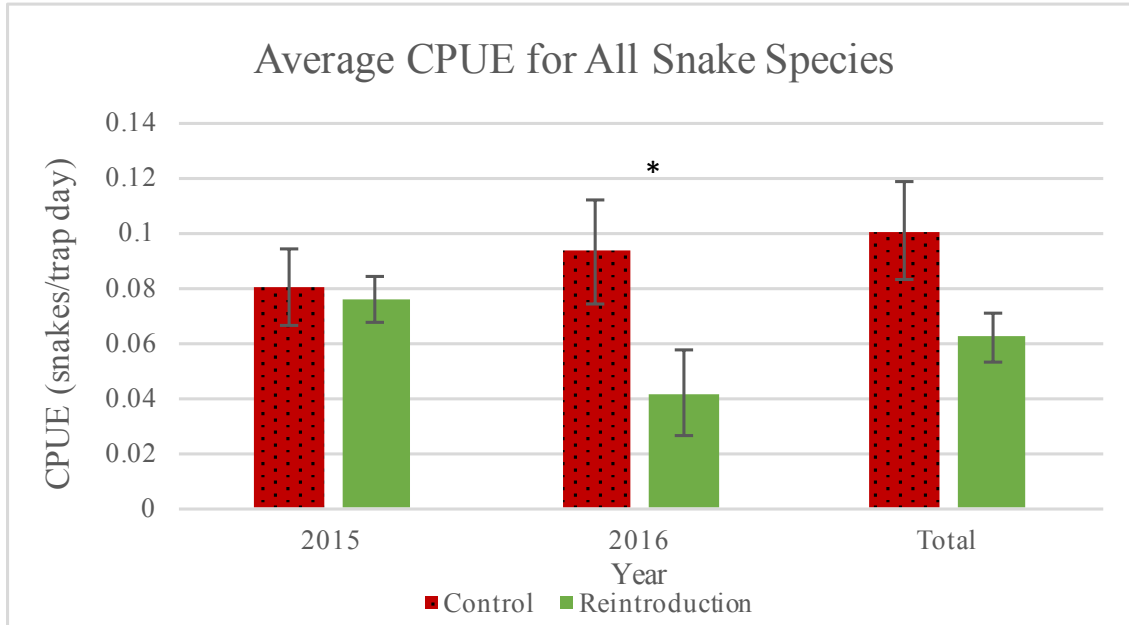


Figure 5: Average Capture Rates for All Snake Species in Control and Reintroduction Sites

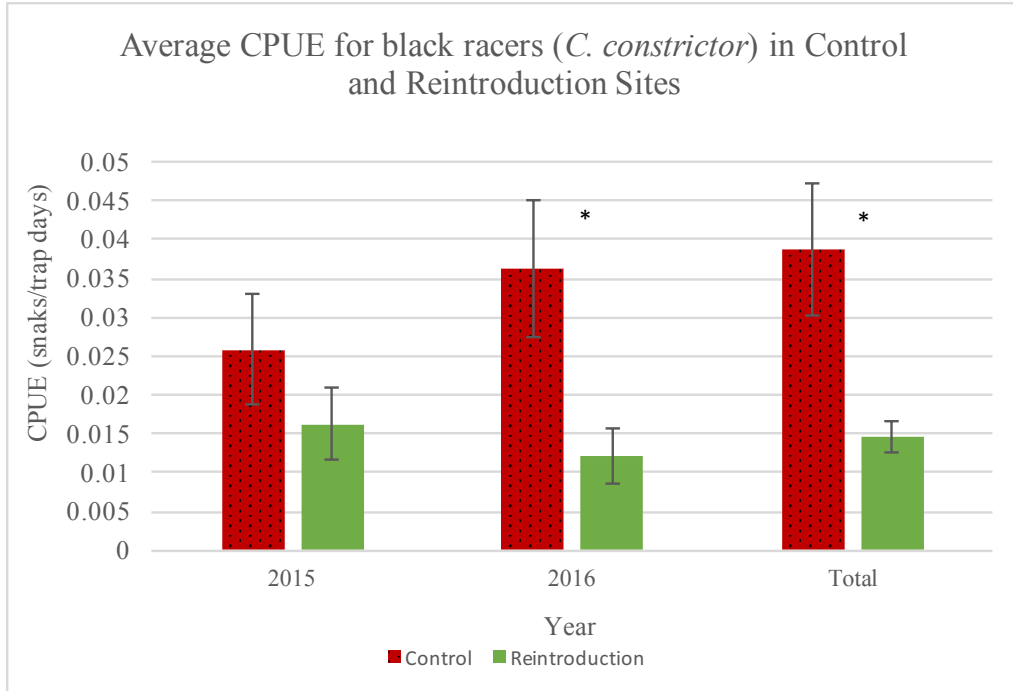


Figure 6: Average Capture Rates for Black Racers (*C. constrictor*) in Control and Reintroduction Sites.

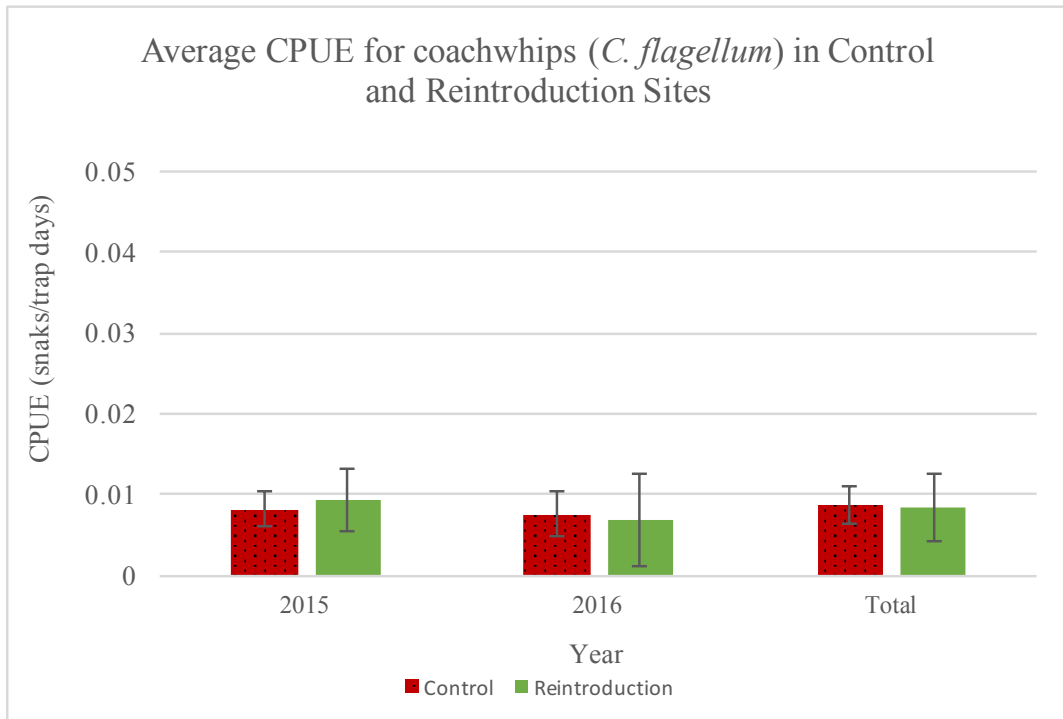


Figure 7: Average Capture Rates for Coachwhips (*C. flagellum*) in Control and Reintroduction Sites.

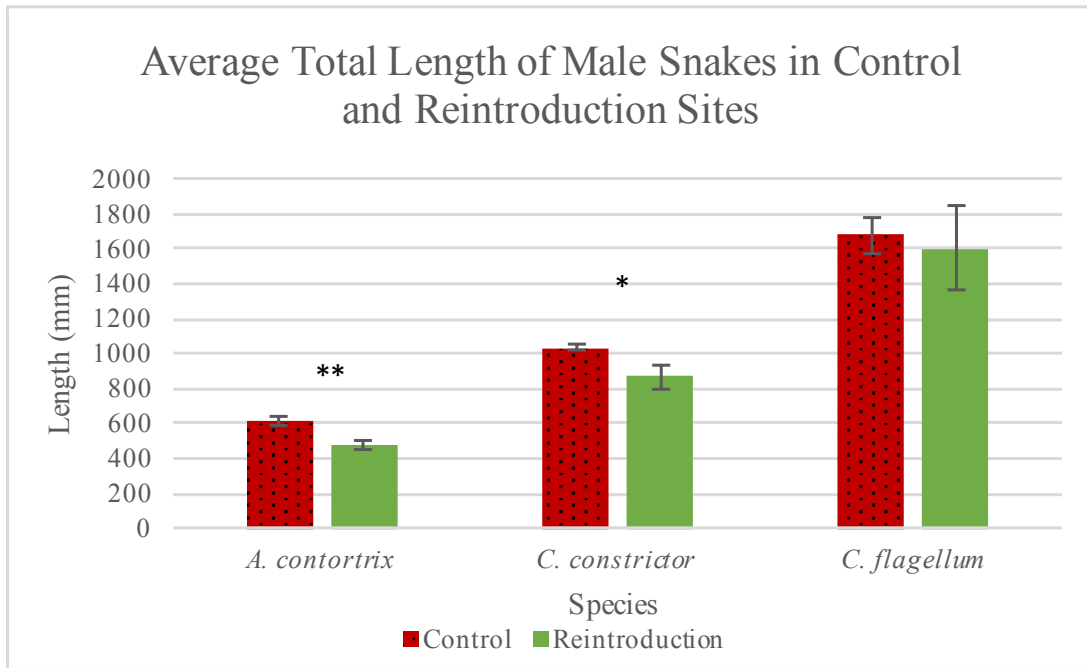


Figure 8: Average Total Length of Male Snakes in Control and Reintroduction Sites

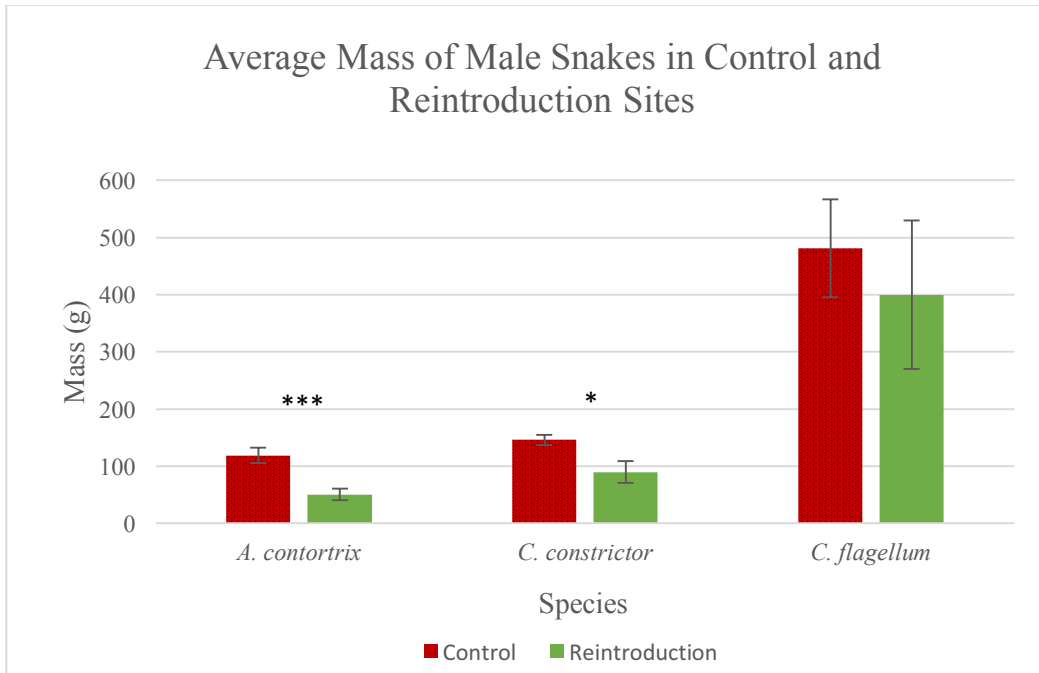


Figure 9: Average Mass of Male Snakes in Control and Reintroduction Sites

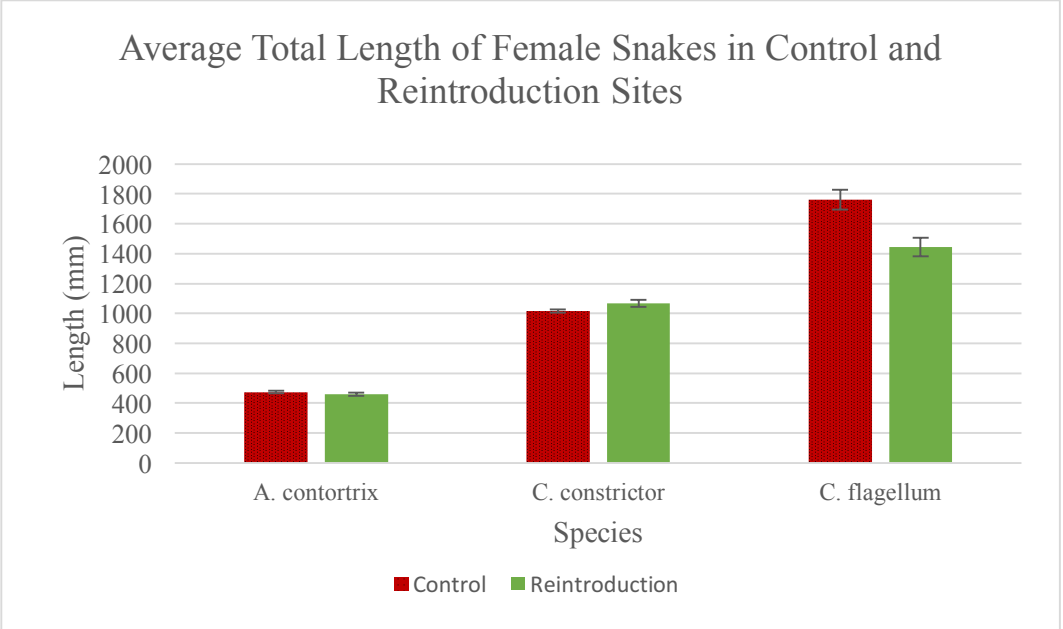


Figure 10: Average Total Length of Female Snakes in Control and Reintroduction Sites

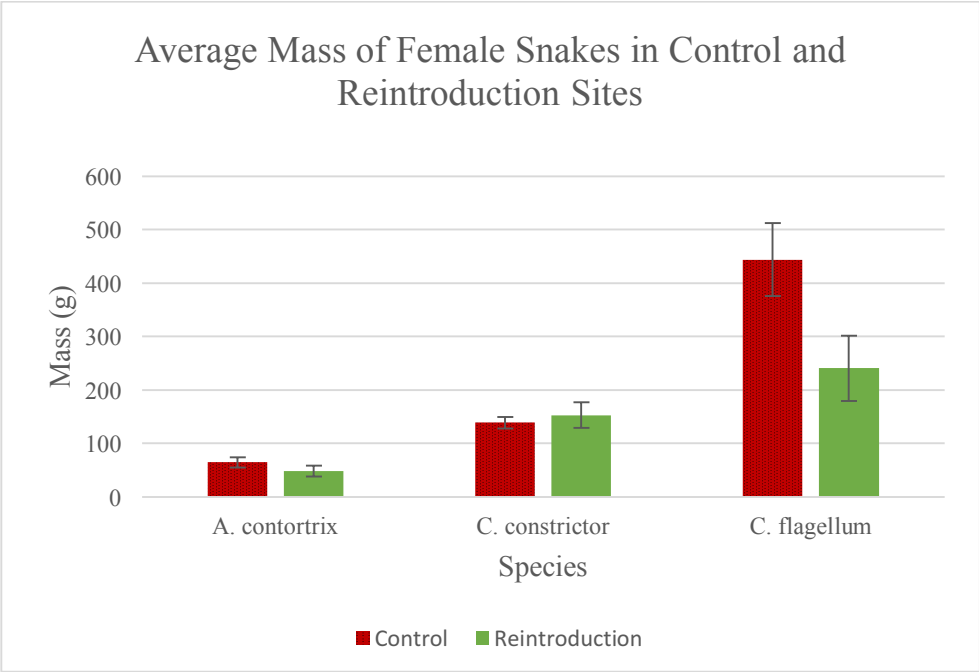


Figure 11: Average Mass of female Snakes in Control and Reintroduction Sites

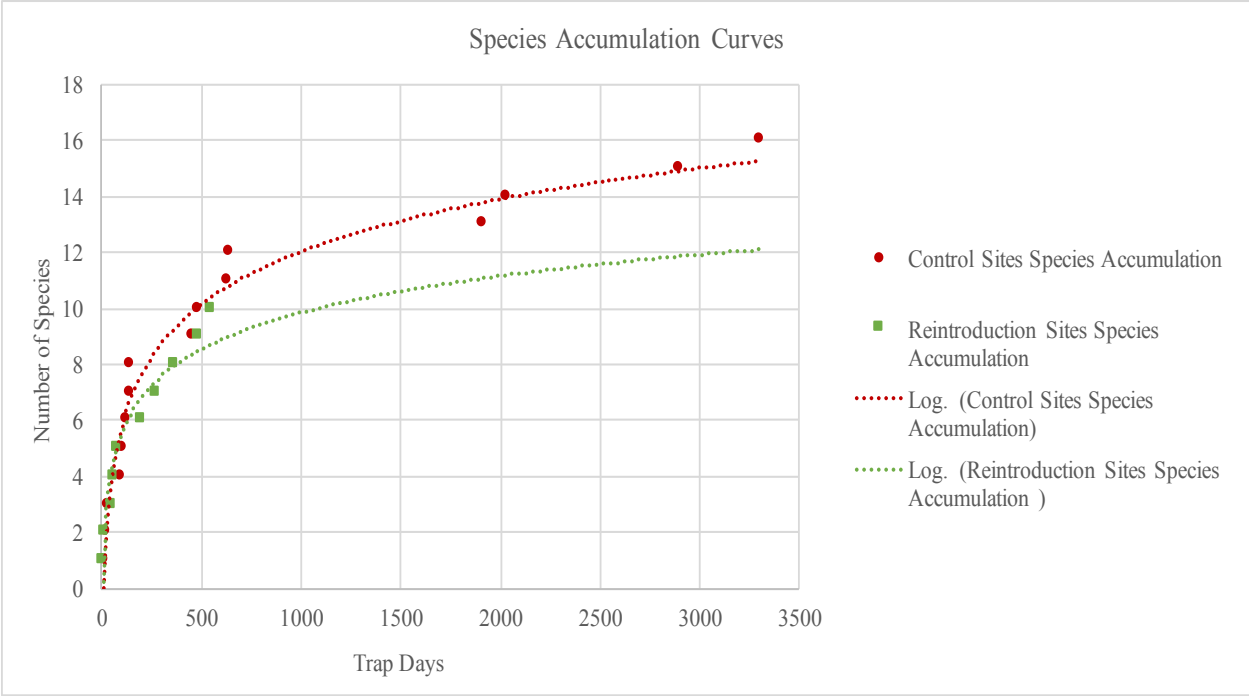


Figure 12: Species Accumulation Curves in the Control and Reintroduction Sites