

## ABSTRACT

BROWN, CHRISTINE LADONA. Spatial Ecology and Conservation of Predators in Fragmented Landscapes. (Under the direction of Nicholas M. Haddad).

Corridors, linear areas connecting two or more habitats, are a conservation method designed to mitigate the effects of habitat fragmentation and facilitate species movement by increasing connectivity between fragmented habitats. Corridors are exceedingly popular for conservation because they are a potential bargain: The connection could provide the benefits of a large continuous landscape, but with a minimal amount of habitat. However, it is still unknown whether corridors work as proposed and most research has focused on single species movement and not on the factors that affect entire communities. In my dissertation, I investigate ways in which corridors can promote biodiversity beyond looking at the movement of a single species. Ecological processes such as predator-prey dynamics should be maintained in otherwise isolated populations by providing increased movement of prey, or food web subsidies. Without maintaining these ecological processes, corridors are destined to reduce diet breadth and trophic stability and reduce the populations they are designed to protect.

My dissertation has three aims: 1. To test if corridors facilitate food web subsidies; 2. To test if corridors increase predator body condition; and 3. To test if corridors increase fecundity. I tested the effect of connectivity on food web subsidies in experimental landscapes at the Savannah River Site in Aiken, SC, designed as a corridor movement study. There are 8 landscapes designed as a movement experiment by introducing an element into a central habitat patch and measure movement to peripheral connected and unconnected patches. To test for trophic subsidies, we enriched flowering plants in the center patch with a

$^{15}\text{N}$  stable isotope to trace through the food web and collected green lynx spiders (*Peucetia viridans*), an ambush predator that hunts on flowering plants, in peripheral patches. I then tested for  $^{15}\text{N}$  enrichment between spiders in corridor-connected and unconnected habitat patches 150m away from the sprayed patch. If corridors facilitate food web subsidies, then spider  $^{15}\text{N}$  in connected patches should be higher than those found in isolated habitats. I collected green lynx spiders within connected and unconnected patches to test the effect of connectivity on body condition by measuring lipid content. Finally, I collected egg sacs and measured spider clutch size. I used novel approaches to test not only species movement, but also the flow of energy from connected and unconnected terrestrial habitat patches. Overall, my work shows that corridors can be advantageous even for predators that do not use the corridor themselves, but rather have enhanced nutrition by an influx of prey.

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Spatial Ecology and Conservation of Predators in Fragmented Landscapes

by  
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North Carolina State University  
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requirements for the Degree of  
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## **DEDICATION**

For my father, Rev. Dr. George Brown, who received his PhD two months before I was born,  
and passed away two months before I received mine.

## BIOGRAPHY

I knew I wanted to be a biologist when I was 10 years old. An older couple in my hometown in Arizona started a biology camp, which was really an excuse to take kids out on field trips to explore gorgeous desert landscapes and dissect things (baby sharks and fetal pigs!). I was hesitant because none of my friends were going, but my parents, who preferred to enjoy natural beauty from the other side of a window, saw this as an opportunity finally let me free to roam our wild surroundings. I was shy as first, but I was sold after finding a recently dead bullfrog at the bottom of a hot spring. My prepared biology hosts had a dissection kit on hand, and I can still remember the thrill and wonder of being able to make my first discoveries. It was a twelve inches long! It had eggs! Its leg muscles look remarkably like mine. I learned that day that I could be rewarded by stopping and observing the world around me; mysteries were just waiting to be found. Little did I know at the time that making simple observations was the foundation of ecology.

The skill of observation remained important for me as an undergraduate at Beloit College. I worked as a research assistant for Dr. Brett Woods at the Rocky Mountain Biological Laboratory, where I researched how yellow-bellied marmots may adapt to climate change by shifting life history characteristics. Through marmot stalking, or observing them with a scope, I found both behavioral and physiological modifications that marmots make in order to prepare for winter under harsh conditions.

Now, eighteen years after the inception of my career ambition, observations helped me expose a case in ecology that is virtually invisible in other systems. I found an abundant predator in an experimentally fragmented landscape that hides in plain sight: spiders. Spiders

turned out to be model organisms for understanding how predators respond connectivity. I could ask questions that people wanted to know about jaguars, but could never answer on something so cryptic and elusive. The greatest tool for science is the same one that I learned at 10 years old. I wonder what I will see next.

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**CHAPTER 1: Stable isotope tracing reveals corridors provide food web subsidies to predatory spiders**

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**ABSTRACT**

Corridors are a conservation method to facilitate species movement by increasing connectivity between fragmented habitats. Ecological processes such as predator-prey dynamics are expected to be maintained in otherwise isolated populations by providing food web subsidies. Without maintaining these ecological processes, corridors are destined to reduce diet breadth and trophic stability. Yet, corridor research has focused on single species movement and not on the factors that affect trophic dynamics. My study was designed to test two aims: (1) whether stable isotope marking is an effective method to trace food web connections in a terrestrial field setting (2) whether corridors facilitate food web subsidies. We tested the effect of connectivity on food web subsidies in experimental landscapes at the Savannah River Site in Aiken, SC, designed as a corridor movement study. We have 8 landscapes designed as a movement experiment by introducing an element into a central habitat patch and measure movement to peripheral connected and unconnected fragments. To test for trophic subsidies, we enriched flowering plants in the center patch with

a  $^{15}\text{N}$  stable isotope to trace through the food web and collected green lynx spiders (*Peucetia viridans*), an ambush predator that hunts on flowering plants, in peripheral fragments. We then tested for  $^{15}\text{N}$  enrichment between spiders in corridor-connected and unconnected habitat fragments 150m away from the sprayed fragment. If corridors facilitate food web subsidies, then spider  $^{15}\text{N}$  in connected fragments should be higher than those found in isolated habitats. We collected green lynx spiders within connected and unconnected fragments to test the effect of connectivity on abundance.

We found that enriching  $^{15}\text{N}$  into plant communities did enrich  $^{15}\text{N}$  of spiders as compared to negative control spiders. The enrichment in spiders was consistent across individuals and four times the  $^{15}\text{N}$  of negative control spiders. We conclude that using  $^{15}\text{N}$  is an appropriate mark for food web studies. For aim 2, we found that spiders in connected fragments had a 40% increase compared to their pre-enrichment, whereas unconnected fragments had no significant increase in  $^{15}\text{N}$ . For aim 3, we found that spiders in corridor-connected fragments had almost twice the lipid content as spiders in unconnected fragments. Our results demonstrate that corridors are responsible for increasing prey movement through a mosaic of habitats and that we can successfully trace prey movement via predator consumption of  $^{15}\text{N}$  and that these subsidies have benefits to spider body condition. This is one of the few studies to test for community-level effects of corridors and shows that they support food web dynamics at the landscape scale.

## INTRODUCTION

Food webs are rarely confined within a single focal area and local patterns and dynamics are often driven by factors outside the system (Baxter et al. 2004; Marczak et al. 2011; Rand et al. 2006; Huxel & McCann 1998). This complexity within food webs can maintain community-level traits and buffer against trophic cascades and ecosystem instability (Polis et al. 1997; Holyoak & Sachdev 1998). However, in fragmented landscapes, the movement of nutrients, energy, and prey are likely limited, making cross-boundary resources, or spatial subsidies, more important for organism growth and reproduction, particularly for consumers (Layman et al. 2007).

Predators, at the top of the food chain, are the first taxa to disappear from fragmented landscapes. Predators are sensitive to habitat fragmentation because resource requirements increase with trophic level (Holt et al. 1999). As fragments decrease in size, resources become more limited. Predators rely on prey for growth, development and reproduction. Increasing the flow of resources between habitats, or food web subsidies, could increase fitness for predators in fragmented habitats (Ulanowicz et al. 2013). This is driven largely by limited access to mates and the depletion of prey (Ripple et al. 2014), so it is essential for predator-specific conservation action to include management actions that increase connectivity of the entire food web.

One potential solution for increasing spatial subsidies is implementing landscape corridors; strips of habitat connecting otherwise isolated fragments. Corridors have been the most widely adopted conservation strategy for mitigating the effects of habitat fragmentation

(Taylor et al. 1993, Hilty et al. 2006). While corridors have been implemented around the world, concerns remain regarding their effectiveness across species and habitats (Haddad et al. 2014). This is partially because many corridor studies lack appropriate controls to effectively test for connectivity (Gilbert-Norton et al. 2010; Gregory & Beier 2014). The majority of corridor studies test effectiveness through individual movement or, in rare cases, gene flow (Gilbert-Norton et al. 2010; Gregory & Beier 2014). These studies are critical to understanding if corridors achieve our main conservation goals; however, because these studies often focus on a single species, it is difficult to project these results onto entire communities.

Corridors that provide food web subsidies could allow predators to supplement their local prey, thus increasing resource availability. In classic food web subsidies systems, predator fitness can be decoupled from local productivity, allowing them to survive even in low productivity habitats. Polis and Hurd (1996) found that food web subsidies from the highly productive marine food web were able to sustain consumers from the low productive terrestrial island food web. Similarly, Baxter et al (2004) found that the density of tetragnathid spiders, from the terrestrial food web, plummeted when stream subsidies, aquatic insects, were experimentally removed. These studies measure predator success in population size, but it can also be measured in macronutrient content, or the essential nutrients that individuals use for growth, reproduction, and survival (Mayntz & Toft 2001; Mayntz et al. 2009). Predator success at habitat boundaries can be dependent on the flow of prey (Martinson & Fagan 2014).

Wildlife corridors are generally designed to increase the movement of the focal species to increase access to mates and breeding habitat. However, because corridors may also increase resource availability, predators can have higher individual fitness via connectivity. We test the role of corridors on providing food web subsidies and then the effect of those potential subsidies by testing macronutrient content of predatory spiders. We created a novel use of the stable isotope  $^{15}\text{N}$  to track spider prey from plant consumption through an experimentally connected landscape to spider bodies. We conducted this experiment in the largest, most well-replicated corridor experiment in the world. This study shows that connectivity in the landscape-scale effects the movement of prey and can be traced using stable isotopes and the distinctly measured in spider physiology.

## **METHODS**

### **Site Description**

We performed these studies at the corridor experiment at the Savannah River Site (SRS), a National Environmental Research Park located in Aiken and Barnwell Counties, South Carolina, USA (33.20N, 81.40W). We restored longleaf pine savanna by clearing mature pine forest into 1 hectare habitat clearings, and seeding with a low density of long leaf pine trees (*Pinus palustris*). We further maintain the savanna habitat by burning the landscapes with low-intensity prescribed fire every 2-3 years. We created 8 1km replicate blocks, each consisting of a central fragment surrounded by four equidistant peripheral fragments, one connected by a 150m long x 25m wide corridor and the other three unconnected. The unconnected fragments differ in shape to test for the role of corridors in creating edge effects: the high edge fragment has a high edge to core ratio; the low edge

fragment has a low edge-to-core ratio. We isolate the effects of connectivity from edge effects by comparing the corridor-connected fragment to the high edge unconnected fragment. All landscapes were separated by at least 1.5 km to minimize the chance of dispersal between them.

## **Species**

We investigated the effects of fragmentation and the role of corridors in providing food subsidies for *Peucetia viridans*, a large cursorial oxyopid that inhabits the open fields of our habitat fragments. *P. viridans* is typically known as an agriculturally beneficial ambush predator, as it feeds pest species like aphids and moth caterpillars, although a significant portion of pollinators (hymenoptera and diptera) are also in its diet. *P. viridans* are generally semelparous (one egg sac per female), but can be opportunistically iteroparous (multiple egg sacs) with increased food resources or loss of an egg sac (Fink 1986). They are annual species that develop over eight molts through spring and summer, become reproductively mature in July and August, and create egg sacs in September and October. Adult females guard egg sacs for 6-8 weeks until the clutch balloons as second instars (Fink 1986). They are locally abundant in our fragments and do not differ in abundance by fragment shape (personal observation).

## **Trophic tracer method - Confirming enrichment from plants to spiders**

To test the movement of signal produced by  $^{15}\text{N}$  tracer in spiders after enriching plants, we conducted a study to track its concentration through the food web. Following the enrichment protocol developed for tracking seed dispersal, we enriched flowers of plants that were frequented by *P. viridans* with a solution of 0.125 g/l  $^{15}\text{N}$ -urea (98.9 atom%; Sigma-

Aldrich, St. Louis, MO, USA), water, and one drop of Tween20 (Sigma-Aldrich, St. Louis, MO, USA) to reduce surface tension and improve contact to plant tissue (Carlo et al. 2009; Forster & Herrmann 2014). We sprayed inflorescences using a handheld pump sprayer with a fine mist nozzle. Each plant received enough solution to saturate each flower petal, about 13 ml. To limit airborne drift and evaporation, we sprayed plants on days with no wind or prior precipitation, completed spray treatments prior to 10:00, and sprayed in a downward-facing angle.

We sprayed all flowering plants located in a 25m by 10m area of a 50m wide 2km long power line that had similar plant species composition and width as our corridor experiment landscapes in July of 2010.

We hand-collected plants and sweep netted for individuals representing increasing trophic levels based on their known life history. For primary consumers, we collected orthopterans, as they represent one of the most important herbivores in grassland habitats (Evans et al. 2012). For secondary consumers, we collected green lynx spiders, as they are dominant predators in open field habitats (Nyffeler 1987). We collected all arthropods within the sprayed area for positive controls and at 5-10m and 50-60m distances from the sprayed area 6 weeks after the initial spray treatment. We swept two 25m long transects at each distance, walking transects at a rate of 25m/min. Sweep net samples were immediately stored in a freezer until sorted to morpho-species.

We tested for the presence of  $^{15}\text{N}$  of arthropod samples by drying them in a drying oven, homogenizing single individuals using a Wig-L-Bug grinder (Dentsply, Elgin, IL, USA), weighed samples to approximately 1mg, and wrapped them in tin capsules (5

x 9 mm, CE Elantech, Lakewood, NJ, USA) for mass spectrometry. All samples were analyzed for  $^{15}\text{N}$  atom% using an elemental analyzer (Costech ECS 4010 CHNSO Analyzer, Coatech Analytical Technologies, CA, USA) connected to a Thermo Scientific ConFlo IV Universal interface (Thermo Fisher Scientific, MA, USA), which served as an inlet to the flow isotope ratio mass spectrometer (Thermo Delta V Advantage; Thermo Fisher). Analyses were performed at the Laboratory for Isotopes and Metals in the Environment at Pennsylvania State University (State College, PA, USA). All stable isotope values are reported in the  $\delta$  notation, where  $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]1000$ , where R is  $^{15}\text{N}/^{14}\text{N}$ .

### **Corridor effects on food web subsidies**

To test for the effects of corridors on providing food web subsidies to spiders in connected and unconnected fragments, we added  $^{15}\text{N}$ -urea to the plants in central habitats using the broad spray method described above and collected green lynx spiders in peripheral fragments. We measured  $\delta^{15}\text{N}$  content in *P. viridans* before and after the tracer addition. Because *P. viridans* has a different diet composition based on molt, we restricted our measurement to adult females (Turner 1979). To compare adult females before and after the tracer addition, we measured  $\delta^{15}\text{N}$  from individuals collected in 2011, prior to spray treatment.

### **Corridor effects on abundance**

To test for the effects of connectivity on spider abundance, I hand-collected green lynx spiders from a 75x75m perimeter of each 1 ha fragment type per block. I walked the perimeter of the sample area and continued 10m towards the fragment center and surveyed that perimeter and continued in 10m increments until I spiraled to the center of the fragment.

I surveyed each block four times in six weeks to follow the assumptions of a closed population with emigration or immigration (Pollock 1982). After collection, we stored spider samples in -5C freezer.

### **Statistical Analyses**

To determine movement of signal produced by  $^{15}\text{N}$  tracer in spiders after enriching plants, we compared control samples to individuals collected within the sprayed area using a Student's t-test. To determine the residence time of  $^{15}\text{N}$  in spiders between our two enrichment treatments, we used a Student's t-test. To determine the effects of corridors on providing food web subsidies to spiders in connected and unconnected fragments, we calculated the mean  $\delta^{15}\text{N}$  per patch on spiders collected before the spray treatment and spiders collected after the spray treatment. Then, we used the before and after  $\delta^{15}\text{N}$  values to compare percent change  $\delta^{15}\text{N}$  in connected and unconnected fragments by performing a generalized linear mixed-effects model, with block identity as a random effect. We weighted each fragment mean  $\delta^{15}\text{N}$  so that fragments with small sample sizes did not disproportionately skew the results. All analyses were performed in R (R Core Team, 2013).

## **RESULTS**

### **Trophic tracer method - Plants to spider enrichment**

We sampled a total of 51 green lynx spiders in control and  $^{15}\text{N}$  addition landscapes. Spiders collected from  $^{15}\text{N}$  addition fragments had significantly enriched  $^{15}\text{N}$  signatures compared to those in negative control fragments (Figure 1-2,  $t = -5.80$ ;  $p < 0.001$ ). Spiders in  $^{15}\text{N}$  addition fragments had a mean enrichment of 8.7‰ whereas spiders in control fragments had a mean  $\delta^{15}\text{N}$  of 2.2‰. Strong evidence for the  $^{15}\text{N}$  signature transferring through

consumptive means was provided by the enrichment depleting almost an order of magnitude in each trophic level and little enrichment by movement within trophic levels even short distances from the source area (see Figure 1-1).

### **Corridor effects on food web subsidies**

Corridors increased  $^{15}\text{N}$  concentrations of spiders in connected fragments. We collected 152 green lynx spiders in 2011 in 40 fragments before  $^{15}\text{N}$  treatment and 357 green lynx spiders in 2013 in 29 fragments after  $^{15}\text{N}$  addition. Corridors increased food web subsidies in connected fragments, as spiders in connected fragments had a 40% increase in  $^{15}\text{N}$ , whereas spiders in rectangular and winged fragments had no significant increase ( $F_{2,11} = 3.056$ ;  $P = 0.032$ ; Fig. 2).

### **Corridor effects on abundance**

There was no effect of connectivity on spider abundance ( $F_{2,22} = 1.24$ ,  $P = 0.38$ ; Fig. 3).

## DISCUSSION

Our results demonstrate that corridors are responsible for increasing prey movement through a mosaic of habitats, and that spiders have better body condition by subsidizing their diet consuming prey originating from the center fragment. Food web subsidies between fragments have the capacity to sustain predators in fragmented landscapes. Use of stable isotopes as a tracer in this experimentally connected ecosystem shows that we were able to mass-mark spider prey by enriching plants. Further, we were able to show the high level of movement enabled by corridors as we detected the  $\delta^{15}\text{N}$  signal in connected fragments, but not in unconnected landscapes. Further, spiders from connected fragments have higher lipid content. This suggests that spiders have better macronutrients in connected than unconnected fragments. The high lipid content suggests that spiders have better macronutrients in connected than unconnected fragments. To our knowledge, this is the first study to successfully trace the origin of prey in a terrestrial system and the first to show that corridors support food web dynamics at the landscape scale. Our work has important implications for predator conservation in fragmented ecosystems.

We were able successfully track prey from the central fragment to connected fragments using our stable isotope tracer method. We were able to identify a clear, distinct  $\delta^{15}\text{N}$  signal in spiders after enriching plants. Spiders likely acquired the signal through consumption of pollinators that have consumed plant material (nectar). The distribution of enrichment found across trophic levels is consistent with this notion; the highest enrichment is found in plants that were sprayed directly, then lower for the secondary trophic levels that

consume plants, then lowest for spiders that acquire the signal indirectly. Our results show that stable isotopes can be used to trace consumption through a food web with a distinctly marked origin.

This method has been used extensively in aquatic systems, particularly because movement is inherent to the flow of water (Schlacher et al. 2005). In terrestrial systems, however, marking using stable isotopes is much more difficult because movement from the source is not predictable as upstream and downstream. The only way the signal can leave the plant is through seed dispersal (Carlo et al. 2009) or consumption, and even then recapturing the signal is difficult because that movement is diffuse across a landscape. Conducting this work within the movement experiment of SRS Corridor project, we were able to show corridors transform isolated fragments into a single community linked by movement and consumption.

We found that spiders in corridor-connected fragments had higher  $\delta^{15}\text{N}$  enrichment than those in unconnected fragments. This suggests that there may still be movement related to edge effects; however, this trend was negligible compared to the 39.7% increase found in spiders in the connected fragments.

The enrichment found in spiders in connected fragments is likely caused by movement of enriched prey rather than enriched spiders that have relocated from source to connected fragments. Spiders rarely move at the landscape scale as adults (Samu et al. 1999), thus we believe that movement of *P. viridans* between fragments is rare, however; even if it was not as uncommon as we suspect, the enrichment values in the connected fragment were

still an order of magnitude less than spiders in the source patch, so it is unlikely that individuals from the connected fragment are a part of the same population as the source fragment. Also, the 40% increase was not comprised of a few highly enriched individuals, but rather, most spiders collected in the connected fragment had a slightly enriched  $\delta^{15}\text{N}$ . Therefore, because the enrichment in the connected fragments was evenly distributed across individuals, and movement between fragments is rare, we attribute the increase in  $\delta^{15}\text{N}$  to the movement of prey.

This study builds on previous work that, together, illustrates the effects of corridors on entire communities. Through previous studies in our experimental landscape, we have found that corridors also facilitate the movement of butterflies and pollen, and create higher plant species richness in connected fragments (Haddad & Tewksbury 2005; Tewksbury et al. 2002; Damschen et al. 2006). These pollinators are an important prey source for *P. viridans*, as we observed the spiders capture butterflies, wasps, and flies (Nyffeler 1987; Turner 1979). The movement of these primary consumers then serves to disperse pollen through connected landscapes and increase prey resources for predatory spiders. Our data suggest that within this system there are strong bottom-up effects that may support a larger prey community within corridor-connected fragments.

A key question is then to determine whether the success of predators is detrimental to focal prey communities. This study occurred over a decade after creating the fragments, and we have been consistently finding productive primary and secondary populations, in the presence of these predators and more. Therefore, currently, the dynamics are such to support

the predator community without exploiting prey populations, but more long term research is necessary to know if those dynamics will persist.

Polis et al. (1997) suggest that food web subsidies create a donor-controlled dynamic where prey subsidies allow predators to increase locally. Top-down effects occur when predators subsidized by allocthonous prey increase in density and suppress local prey populations. In these scenarios, because predators are presented with a prey source that they cannot overexploit, their success is independent of the constraints of local productivity and prey dynamics. Therefore, prey subsidies allow predators to overexploit resident prey to the point of extinction without threatening its own population. However, this framework is generally used across habitats that vary greatly in productivity, like stream to bank subsidies (Polis et al. 1997; Marczak et al. 2011). Because corridors link similar habitats, their differences in productivity are likely negligible to cause large dynamic shifts, so responses would likely increase prey availability without decoupling local prey communities. Our results support that prey subsidies allow an increase in resources without exploitation because enrichment found in spiders were small amounts across individuals, suggesting that single individuals were basing most of their diet from the local prey population and simply supplemented with prey from the central fragment.

Through using stable isotopes to trace prey movement through our landscape, our study shows corridors not only increase the movement of prey, but also improve fragment quality for predatory spiders. Corridors create food web subsidies for spiders by facilitating prey movement. Our results demonstrate that a measurable proportion of the *P. viridans* diet

is supplemented by consuming prey from corridor-connected fragments and spiders also had higher lipid content, which can increase fitness (Wilder et al. 2013; Raubenheimer et al. 2009). This work in a model system is the first step to understanding how corridors can impact the community ecology of an ecosystem (Gregory & Beier 2014). It suggests that predators, which are sensitive to habitat fragmentation because of prey depletion, can improve fitness through increased movement of prey alone. Further work is necessary to test if these ecological measurements in corridor-connected systems also promote other conservation goals such as gene flow and occupancy, however, many studies have shown direct links from improved physiology and prey availability to increased fitness (Schmidt et al. 2012; Weaver et al. 1996; Gannes et al. 1998; Kreiter & Wise 2001). By using a stable isotope tracer in a large-scale, connected experimental landscape, we provide evidence that corridors increase food web subsidies to predatory spiders. We show that corridors increase the strength of trophic dynamics in fragmented landscapes, not simply the movement of individuals; which shows the effects of corridors span beyond the range of focal species to larger communities.

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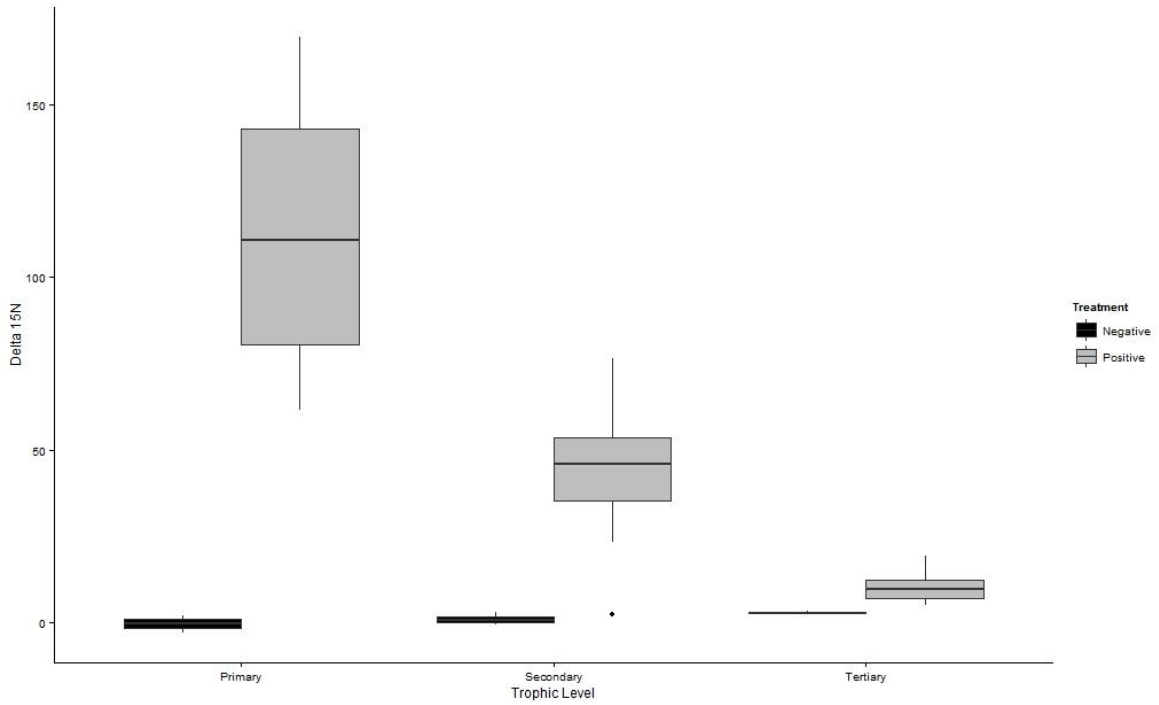


Figure 1-1. Differences in magnitude between  $\delta^{15}\text{N}$  enrichment for different trophic positions. We directly sprayed the primary trophic position, while herbivores and predators obtained the signal through consumption. The difference between positive and negative controls shows that the enrichment was detectable across trophic levels.

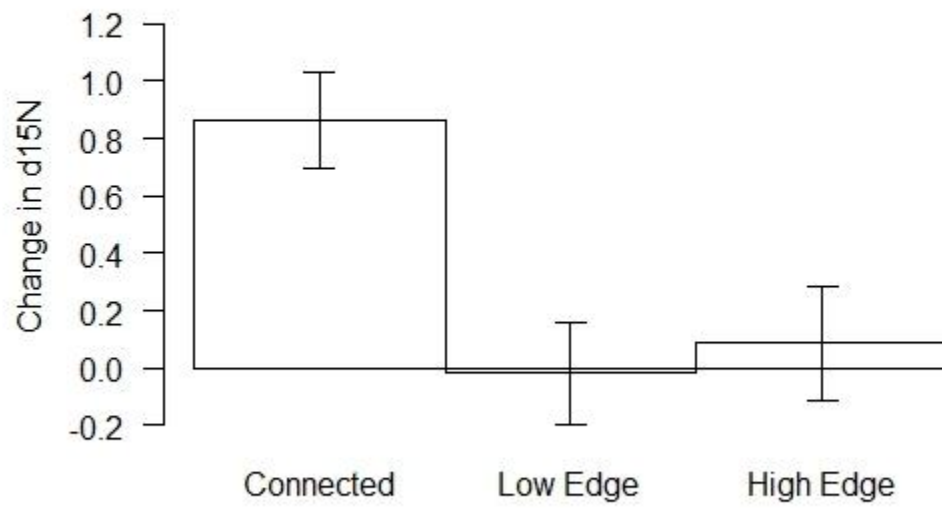


Figure 1-2. The change in  $\delta^{15}\text{N}$  of spiders collected in different fragment shapes before and after spray treatment.

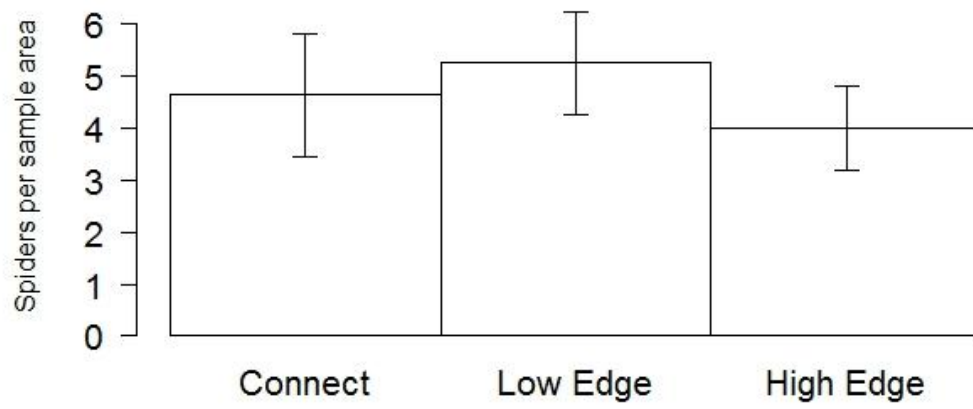


Figure 1-3. Spider abundance by fragment type.

## **CHAPTER 2: Edge effects and connectivity increase predator body condition**

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### **INTRODUCTION**

Habitat loss and fragmentation are considered to be the largest threats to biodiversity (Haddad et al. 2015). Observed declines in biodiversity are determined by the loss of individual populations, and in fragmented landscapes, their rate of extinction can be increased by restricted movement between isolated fragments, and by reduced population size in small fragments (Fahrig & Merriam, 1994; Haddad et al., 2015; Hilty et al., 2006; Ripple et al., 2014). A less explored factor that may be an indicator of declining populations is the body condition, or assessment of physiological state, of individuals within populations (Bonte & De La Peña, 2009). Degraded body condition may reduce aspects of population demography and fitness (Jakob, Marshall, & Uetz, 1996). One factor that may affect body condition and that may be affected by habitat fragmentation is limitations in resource availability (Anderson, 1974; Forsman & Lindell, 1997; Lowe & Peterson, 2014; Navarro-López et al., 2013; Resano-Mayor et al., 2014; Schmidt et al., 2013). Here, I test the effects of fragmentation and connectivity on body condition in a large-scale landscape experiment.

In my experiment, I specifically separate the potentially confounding effects of different aspects of fragmentation. Habitat fragmentation refers to the subdivision of continuous habitat into smaller, more isolated, and edgier areas (Andrén, 1994). Previous

studies have shown that habitat fragmentation decreases body condition across taxa, including spiders and birds, which can reduce fitness and survival (Bucher & Entling, 2011; Lowe & Peterson, 2015; Turcotte & Desrochers, 2008). Because studies of habitat fragmentation are typically not designed experiments to separate fragmentation's effects, as I do here, prior studies of habitat fragmentation effects on body condition have generated contradictory results (Bucher & Entling, 2011; Turcotte & Desrochers, 2008). For example, Bucher and Entling (2011) found that habitat fragmentation, here defined as isolation but not edges, reduced the body condition of one species of spider and had no affect on another. Similarly, Lowe and Peterson (2014) found that high fragment landscapes, defined by their level of urbanization, reduced the body condition of spot and killifish, but supported healthy brown shrimp and blue crab populations. These results support that landscape-scale changes can impact physiology; however, without delineating the confounding effects of fragmentation, inference for conservation action is limited.

One conservation strategy to reduce the effects of fragmentation addresses one element of fragmentation, reducing isolation, by connecting fragments via landscape corridors. Corridors are a popular conservation strategy to mitigate the negative effects of habitat fragmentation by increasing species dispersal (Hilty et al., 2006). However, their efficacy is uncertain because it is logistically difficult to separate the effects of corridors, which are long relative to their width and thus have inherently high edge. Further, corridors increase the area of fragments; therefore it is difficult to determine if corridors are effective because they add connectivity, or simply additional area to a fragment. If not controlled,

observed changes in response to fragment size or connectivity may be confounded with the amount of edge (Ewers & Didham, 2006).

Corridors may increase body condition, and I focus specifically on how they may do so for predators. Corridors have been found to increase connectivity for diverse taxa (Haddad et al., 2003), which can increase the prey availability in fragmented landscapes (Polis, Anderson, & Holt, 1997). However, while there are studies testing the effects of habitat fragmentation on predator body condition (Bucher & Entling, 2011; Diaz & Tellerfa, 1999; Janin et al., 2011; Lowe & Peterson, 2015), there is limited inference for how corridors affect body condition. Atwood et al. (2004) found that coyotes used corridors to move through urban landscapes to higher quality fragments. They suspected, but were unable to test, that coyotes that dispersed through corridors could exploit more prey resources distributed across fragmented landscapes. The effects of corridors on predator body condition remains unknown.

While responses of different species to corridors is unknown, responses of different species, including predators, to edges have been shown to be fairly predictable given their habitat and resource requirements (Ries et al., 2004). Karracker and Welch (2006) found that amphibian body condition decreased in forest fragments with high edge-to-core ratio. Generalist predators may be expected to respond positively to edges because the border of two habitats provides access to multiple prey types (Janzen, 1983; Martinson & Fagan, 2014; Polis et al., 1997; Stamps et al., 1987). For example, Swihart et al. (2003) found that predators with flexible diets were able to adapt to edge habitat by broadening their trophic niche breadth. Further, Martinson and Fagan (2014) found that resource consumption in

arthropod communities decreased in smaller, isolated fragments, but was higher at edges. Edges would be expected to increase body condition of generalist predators.

Predator response to changes in fragment area in fragmented landscapes has been conflicting (Davies et al., 2001; Johnson et al., 2010; Orrock et al., 2003), even within experiments that also test for edge and isolation effects. Fragment area effects are predicted to be strong for predators that avoid (positive) or select (negative) edges, and neutral to generalist species that use both edge and interior (Bender et al., 1998). Davies et al. (2001) found no effect of fragment area on predatory arthropod extinction rate or species richness in an experimentally fragmented forest. Johnson et al. (2010) found higher spider abundance in large fragments than those in small fragments in an experimentally fragmented grassland. Orrock et al. (2003) found that seed predator response to habitat fragmentation was largely dependent on fragment area, not connectivity. The effect of fragment area on predator body condition has not been tested; however, Barbour and Litvaitis (1993) found that rabbits in small fragments had lower body mass than individuals in large fragments. Corridors may have strong positive, negative, or neutral effects on predators as a result of added area, rather than connectivity.

To test the effects of habitat fragmentation on predator body condition, I chose to study spiders as they are conspicuous, abundant model predators that have well-studied physiology. Spiders have been shown to have body condition tightly linked to prey availability (Kreiter & Wise, 2001; Schmidt et al., 2013). Spider allometry, or the relationship between body mass and size, has been shown to respond positively to increases in prey quality and quantity (Schmidt et al., 2013; Wilder, 2013). Further, spiders have been

shown to efficiently extract nutrients from prey, so their nutrient content can reflect the quality of their prey (Mayntz et al., 2005).

I test the effects of habitat fragmentation on predators by measuring body condition in spiders in large-scale landscape experiment that controls for the effects of connectivity, area, and edges. I used morphometrics and macronutrient content to assess body condition, which have been shown to change with prey availability (Schmidt et al., 2012; S. Wilder, 2011). Previous work in our experimental landscapes have shown that corridors increase the movement of bees, wasps, and butterflies, which are all spider prey (Haddad et al., 2003; Turner, 1979); however, there has also been evidence that edge effects and fragment area play important roles in determining species responses to fragmented landscapes (Evans et al., 2012; Orrock et al., 2003). I hypothesize that corridors increase spider body condition by facilitating the movement of their prey. Alternately, predators may have increased body condition by selecting edge habitat to access prey in two different habitat types. Finally, greater fragment area may support more prey, thus increasing predator body condition.

## **METHODS**

### **Site Description**

I tested the effects of habitat fragmentation on body condition at the Corridor Experiment at the Savannah River Site (SRS), a National Environmental Research Park located in Aiken and Barnwell Counties, South Carolina, USA (33.20N, 81.40W). This is a landscape-scale experiment designed to test for the effects of connectivity while controlling for the potentially confounding effects of fragment area and edge. Fragments are restored longleaf pine savanna, a fire-dependent habitat that is native to the southeastern United States

(Frost, 1993). The fragments were restored by opening the canopy of mature pine forest into 1 ha habitat clearings, and seeding with a low density of longleaf pine trees (*Pinus palustris*). The savanna habitat is further maintained by burning the landscapes with low-intensity prescribed fire every 2-3 years, replicating historical frequencies. The matrix is mixed loblolly and longleaf pine plantation, a densely grown and mature forest that has a closed canopy and unproductive understory.

We created 8 replicate blocks, with three treatments and each consisting of a central fragment surrounded by four peripheral fragments (Tewksbury et al., 2002). The Connected fragment is 1ha and connects to the central fragment with a 150m long x 25m wide corridor. Each peripheral fragment is equal to the size of central fragment plus the corridor (1.375 ha), but differs in shape to test for alternative hypotheses of the role of corridors in creating area and edges. The High Edge fragment has two 75m long and 25m wide extensions that do not connect to another fragment, creating a fragment with high edge-to-core ratio that mimics the linear shape of the corridor, but without increasing connectivity. Low edge fragments have a low edge-to-core ratio by adding the area of the corridor (0.375 ha) to the dimensions to the fragment, allowing a test for effects of increased area without also increasing the amount of edge. The experimental landscape is designed to test the effects of habitat fragmentation by separating the potentially confounding effects.

I tested three effects of habitat fragmentation: 1) connectivity effects, 2) edge effects, and 3) area effects (see Table 1). To test connectivity effects hypothesis, independent of edge effects, I compare responses between Connected fragments to High Edge fragments. Predator body condition would be expected to increase because prey movement and/or quality is

facilitated by corridors. To test the edge effects hypothesis, I compare High Edge fragments to Low Edge fragments, both of which are identical in area and unconnected. Predators that prefer edge habitat may be provided access to prey types from two different habitats. To test the area effects hypothesis, I compare the Low Edge fragment to the Connected fragment. This hypothesis would be supported if predator body condition increases in low edge-to-core areas, with one potential mechanism that prey avoid edges.

### **Study Species**

I tested the effects of fragmentation and the role of corridors in predator body condition for *Peucetia viridans* (*green lynx*), a large cursorial oxyopid that inhabits the fragments. They have one generation per year and develop to adulthood in the summer, then become reproductively mature in July and August. Green lynx spiders are habitat specialists and diet generalists: they prefer the open longleaf pine savanna habitat over the pine plantation matrix, and consume more than 30 different arthropod species (Randall, 1982). Green lynx spiders have been important predators in agricultural systems as biocontrol for pest species such as aphids (Nyffeler, 1987). Their main prey are bees, wasps, flies, and butterflies (Turner, 1979), which have been found to increase dispersal in corridor-connected fragments (Haddad et al., 2003). They are locally abundant in our patches and are distributed equally across fragment shapes (Brown, Chapter 1).

### **Collection**

I hand-collected green lynx spiders and their egg sacs from one Connected, High Edge, and Low edge fragment in each block. I performed four surveys within six weeks to assume a closed population of no immigration or emigration between surveys (Pollock,

1982). I sampled each fragment for 1.5 hours and surveyed the central 75x75m area by beginning at 12.5 m away from the fragment edge, then searched the 75m perimeter of the fragment. I then moved ten meters towards the interior and searched that 65 meter perimeter and repeated until I circled to the fragment center. The spiraling survey allowed me to quickly cover the most area while remaining thorough. After collection, I immediately stored spiders in a -5 °C freezer. My goal was to collect 10 spiders per fragment, or a total of 240 spiders.

### **Body Condition**

I measured a range of morphological traits to test the effects of habitat fragmentation on spider size and to generate multiple measures of condition. To compare body size, I measured cephalothorax width, which is a typical measure for spiders (Jakob et al., 1996), to the nearest 0.01 mm using a DinoCapture 2.0 digital microscope (Version 1.3.8, Dino Lite Microscopes; Naarden, The Netherlands). I measured the dry mass of spiders to the nearest 0.01 mg, first drying samples for >48 hours at 40 °C. I compared body condition using the Residual Index, a body condition metric found to most accurately control for variation across body size in spiders (Jakob et al., 1996). I first calculated the regression of logarithmic transformed body mass on the logarithmic transformed body size:

$$\ln(\textit{body mass}) \sim \ln(\textit{body size})$$

The estimate for condition was the residual distances of individual points from the regression line.

To test the effects of habitat fragmentation on spider nutrient content, I measured isotopic nitrogen ratios (<sup>15</sup>N:<sup>14</sup>N). The nitrogen ratio,  $\delta^{15}\text{N}$ , has been shown to be negatively

related to body condition because when starving, animals consume their own  $^{14}\text{N}$ , thereby increasing the ratio of  $^{15}\text{N}:$  $^{14}\text{N}$  (Colborne & Robinson, 2013; Oelbermann & Scheu, 2002). I processed samples for carbon and nitrogen by first homogenizing single individuals using a Wig-L-Bug grinder (Dentsply, Elgin, IL, USA), weighed samples to approximately 1mg, and wrapped them in tin capsules (5 x 9 mm, CE Elantech, Lakewood, NJ, USA) for mass spectrometry. All samples were analyzed for  $^{15}\text{N}$  atom% using an elemental analyzer (Costech ECS 4010 CHNSO Analyzer, Coatech Analytical Technologies, CA, USA) connected to a Thermo Scientific ConFlo IV Universal interface (Thermo Fisher Scientific, MA, USA), which served as an inlet to the flow isotope ratio mass spectrometer (Thermo Delta V Advantage; Thermo Fisher). Analyses were performed at the Stable Isotope Laboratory at the University of California, Davis (Davis, CA, USA). All stable isotope values are reported in the  $\delta$  notation:

$$\delta^{15}\text{N} = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] 1000$$

where  $R = ^{15}\text{N}/^{14}\text{N}$ . The  $R_{\text{standard}}$  used was universal bovine.

Because nitrogen has long been thought to be a limiting nutrient in predators, C:N ratios are also inversely related to body condition (Denno & Fagan, 2003); however, because not all nitrogen is acquired and allocated for consumption, the credibility of the metric has recently been debated (S. M. Wilder & Eubanks, 2010). I processed these samples using the same protocol as the stable isotope samples, and calculated C:N ratio

$$\frac{\%C \times Mass}{\%N \times Mass}$$

To measure lipid content, I extracted chloroform gravimetrically (Wilder et al., 2010). Briefly, I soaked samples in 2ml of chloroform for 24 hours and repeated twice. I then reweighed samples to calculate the difference in mass before and after lipids were extracted by the chloroform.

### **Statistical Analyses**

To determine the effects of connectivity on body condition, I used linear mixed-effects models, with block as a random effect and fragment shape as a fixed effect. Fragments are the experimental unit in this experiment, thus I calculated the mean response per fragment for each metric as to prevent pseudo-replication. For each significant model, I performed planned paired contrasts to test the hypotheses regarding connectivity, edge, and area effects of fragmentation (see Table 2-1) using a least-squares means tukey test. This test estimates the predicted response of fragment shape given specified body condition measurement. For each effect, I compare the Connected fragments to the High Edge fragments to test the effects of connectivity, the High Edge fragment to the Low Edge fragment to test for edge effects, and the Connected fragment to the High Edge fragment to test for area effects.

## **RESULTS**

I collected a total of 357 green lynx spiders from 24 experimental fragments. Most measures of body condition supported the area effects hypothesis (see Table 2-2). The area effects hypothesis was supported by approximately equal estimates in body size, mass, residual index (see Figure 2-4), and  $\delta^{15}\text{N}$  (see Figure 2-1), respectively, across all fragment types, suggesting an edge-neutral response. The fragment area hypothesis was supported by a

significant negative effect of area on C:N ratio ( $F_{2,21} = 5.96, p = 0.0089$ ; see Table 2-2), however, it followed predictions expected for edge-selecting spiders. Connected fragments had a significantly lower C:N ratio than in Low Edge fragments ( $t = -4.6, p > 0.001$ ), but was not significantly different from High Edge fragments (see Figure 2-1). The connectivity hypothesis was supported by a strong positive effect on lipid content ( $F_{2,19} = 6.55, p = 0.0069$ ; see Figure 2-3). Spiders in Connected fragments had twice the lipid content as those in High Edge fragments ( $t = 3.57, p = 0.01$ ), while lipid content of spiders did not differ between those in High and Low Edge fragments.

## DISCUSSION

Corridors most often affected the body condition of predators in a way that is predicted by area effects, suggesting that the area corridors add to fragments is more important than connectivity. Spiders in these fragmented landscapes showed no response to habitat fragmentation in most metrics of body condition, suggesting that because response estimates were similar across fragment types, green lynx spiders use both interior and edge habitats to acquire resources. However, some measures of body condition showed strong positive changes to spider body condition in corridor-connected fragments. I suggest that because all metrics were in the same individual, the variation in responses may be a result of metrics not being sensitive enough to detect changes body condition, rather than the different responses to habitat fragmentation.

One way that connectivity had a strong positive effect on body condition independent of area effects was on spider lipid content, the measurement that is directly related to resource acquisition (Wilder, 2011). Spiders in corridor-connected fragments had twice the

lipid content as those in High Edge fragments. Lipids are directly extracted from prey and from accumulating carbohydrates in metabolism, and are therefore a more accurate measure of consumption than another commonly used metric for body condition in spiders, allometry (Raubenheimer et al., 2007). Allometry, however, represents a measure for growth which individuals can invest finite resources that can be allocated to growth, maintenance, or reproduction (Stearns, 1989). Allometry represents an investment in individual growth, whereas lipids represent the amount of resources available for total allocation (Post & Parkinson, 2001). Lipids are a key nutrient that predators need to build energy reserves to survive periods of food limitation and invest in reproduction (Jensen, Mayntz, Wang, Simpson, & Overgaard, 2010; S. Wilder, 2011). My results showing increased lipid content in Connected fragments show that corridors facilitate an accumulation of fat reserves for green lynx spiders. In the context of applied conservation, this implies that by simply adding corridors between fragments, spiders can have increased fitness.

Another measure of internal body condition,  $\delta^{15}\text{N}$  did not vary by fragment shape, but showed a marginally non significant effect of connectivity. While not conclusive on its own, coupled with the result of high lipid content, it does suggest that there may be differences in prey consumption that causes Connected fragments to have depleted  $\delta^{15}\text{N}$ . In addition to consuming their own fat reserves, individuals that are starving consume their own  $^{14}\text{N}$ , leaving enriched  $\delta^{15}\text{N}$  signals (Anderson, 1974; Oelbermann & Scheu, 2002). Because spiders in isolated fragments had almost half the lipid content as those in Connected fragments, my results support that  $\delta^{15}\text{N}$  enrichment in both High and Low Edge fragments could mean that spiders in those fragments are manifesting a sign of starvation. More work

on the direct comparison of consumption in connected and unconnected fragments is necessary to understand how corridors may influence spider food availability in fragmented landscapes.

Corridors had a strong negative effect on spider C:N ratios, suggesting that spiders respond to the added area of corridors. Spiders in corridor-connected fragments had a lower C:N ratio than those in Low Edge fragments; however, they were not significantly different from estimates in High Edge fragments, which suggests that spiders prefer edge habitat (see Table 1). Low C:N ratios reflect better body condition, as nitrogen has been hypothesized to be a limiting nutrient for predatory arthropods and serves as a proxy for protein and amino acids (Denno & Fagan, 2003). However, there has been growing support that nitrogen is not an accurate measurement of body condition because proteins vary in their amount of nitrogen (Lourenço, Barbarino, De-Paula, Pereira, & Lanfer Marquez, 2002; S. M. Wilder & Eubanks, 2010). Further, nitrogen in arthropods is used in more contexts than simply diet and body maintenance, as sclerotized body parts and pheromones also contain and require nitrogen (Raubenheimer, Simpson, & Mayntz, 2009). Low C:N ratio in Connected and High Edge fragments suggests that spiders are able to acquire more essential nutrients in prey sources than in High Edge fragments, however, a direct measurement of protein content would further delineate this result as it pertains to prey acquisition.

Corridors have been found in previous studies to have complex effects on ecological interactions (Orrock et al., 2003). These species-specific responses to habitat fragmentation will alter food-web dynamic across the landscape (Polis et al., 1997). Previous work in these landscapes have shown Low Edge fragments have increased herbivory relative to Connected

and High Edge fragments, because ground-dwelling invertebrates prefer interior habitat (Evans et al., 2012). However, Corridors have been found to increase the dispersal of pollinators, the main prey items of green lynx spiders, in fragmented landscapes (Haddad et al., 2003). While the reported increases in spider prey movement likely increase prey availability in Connected fragments, a direct measurement of consumption is necessary to identify the mechanism that drives increases (Forsman & Lindell, 1997).

Corridors have been shown to have both positive and negative ecological effects on fragmented landscapes (Haddad et al., 2014). If the target for conservation is a predator, my work provides a framework in which corridors have the potential to provide resources for predators to accumulate fat reserves. Fat reserves can enable predators to be more robust to environmental or stochastic changes, thus increasing their likelihood of persistence (Bommarco, 1998). However, if predators prey on the conservation target, my work also shows that predators are able to either acquire or retain more fat reserves in corridor-connected fragments, which may have negative effects on prey populations (Simberloff et al., 1992). However, the effect of predators on prey populations is dependent on more than the number of predators. Predators have both consumptive and non-consumptive effects on prey populations, and in fragmented landscapes can change the dynamics of metapopulation persistence (Orrock et al., 2008). Predators can both exploit prey to extinction, or promote prey dispersal between fragments, which can increase prey persistence (Gilliam & Fraser, 2001; Swihart et al., 2001). Further, predators shape communities, as effects on prey populations cascade through the food web (Schmitz et al., 1997). By increasing predator body condition, corridors can alter food web dynamics in fragmented landscapes.

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Table 2-1. Tested hypotheses and predictions for connectivity, edge, and area effects.

Effect	Description	Predicted Outcome
<b>Connectivity effects</b>	Predator body condition increases because prey movement and/or quality is facilitated by corridors	Conn > High Edge; High Edge ≈ Low Edge
<b>Edge effects</b>	Predators prefer edge habitat that provides access to prey types from two different habitats	High Edge ≈ Conn; High Edge > Low Edge
<b>Area effects</b>	Corridors increase both the amount of habitat and edge-to-core ratio. Effects are dependent on the predators response to edge:	
	edge-avoiding	Low Edge > Conn; Conn ≈ High Edge
	edge-neutral	Conn ≈ High Edge ≈ Low Edge
	edge-selecting	Conn > Low Edge; Conn ≈ High Edge

Table 2-2. The effects habitat fragmentation on six body condition metrics.

<b>Body Condition Metric</b>	<b><i>F</i></b>	<b><i>df</i></b>	<b><i>P</i></b>	<b>Hypothesis Supported</b>
<b>Body Size</b>	1.56	2,21	0.238	Area - Edge Neutral
<b>Mass</b>	1.84	2,21	0.184	Area - Edge Neutral
<b>Residual Index</b>	0.08	2,21	0.920	Area - Edge Neutral
<b><math>\delta^{15}\text{N}</math></b>	2.94	2,22	0.074	Area - Edge Neutral
<b>C:N Ratio</b>	5.96	2,21	0.009	Area - Edge Selecting
<b>Lipid Content</b>	6.55	2,19	0.007	Connectivity

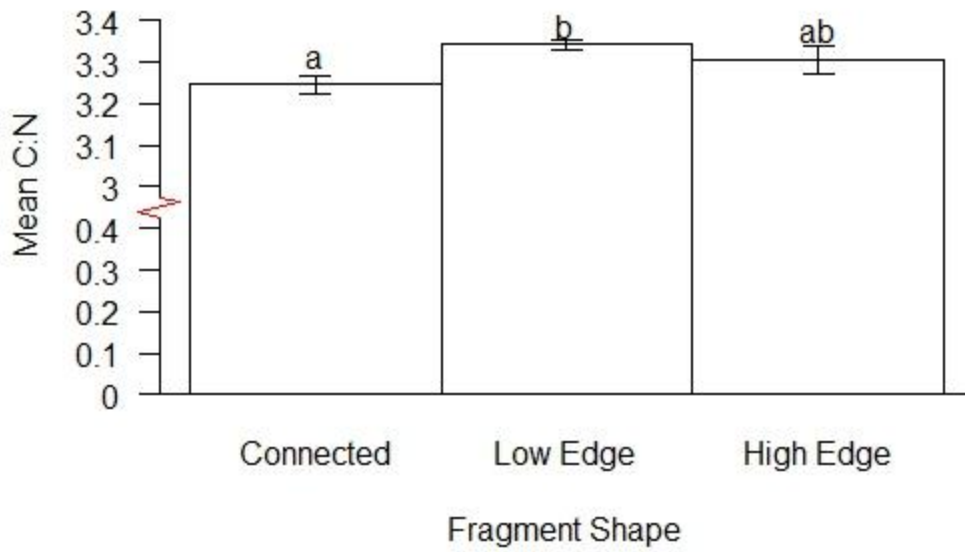


Figure 2-1. The Carbon:Nitrogen ratio in spiders by fragment shape. Corridor-connected fragments had significantly smaller C:N ratios than Low Edge fragments, supporting the area effects hypothesis.

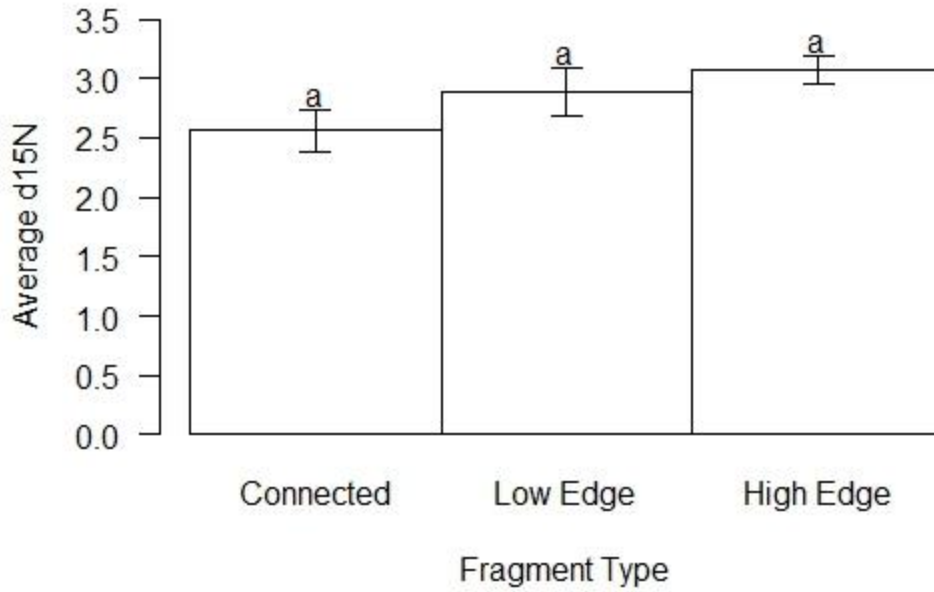


Figure 2-2. The mean  $\delta^{15}\text{N}$  in green lynx spiders by fragment type. While there was no statistical difference between fragments types, the enrichment in High Edge fragments may be a result of starvation.

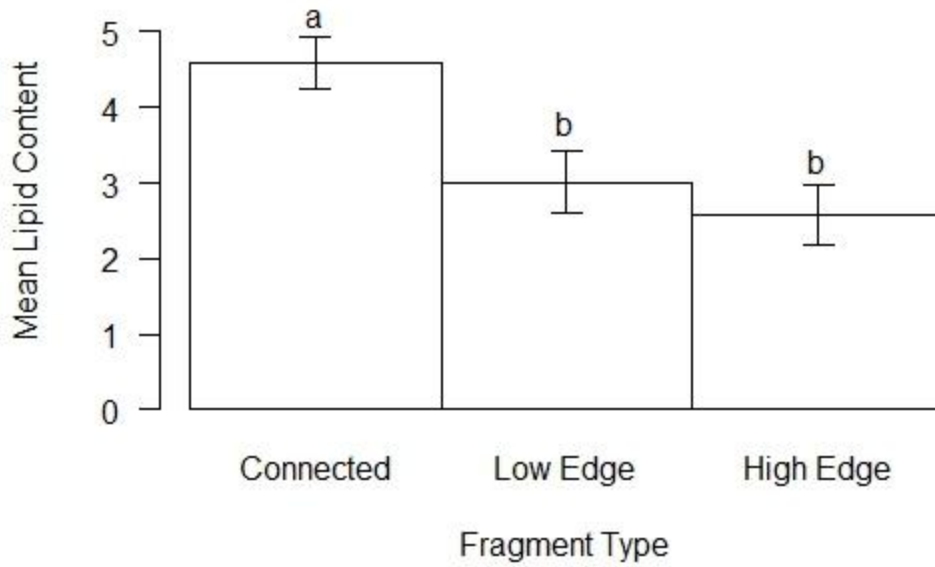


Figure 2-3. Mean lipid content by fragment type. Spiders in corridor-connected patches had almost twice those in High Edge fragments, supporting the connectivity hypothesis.

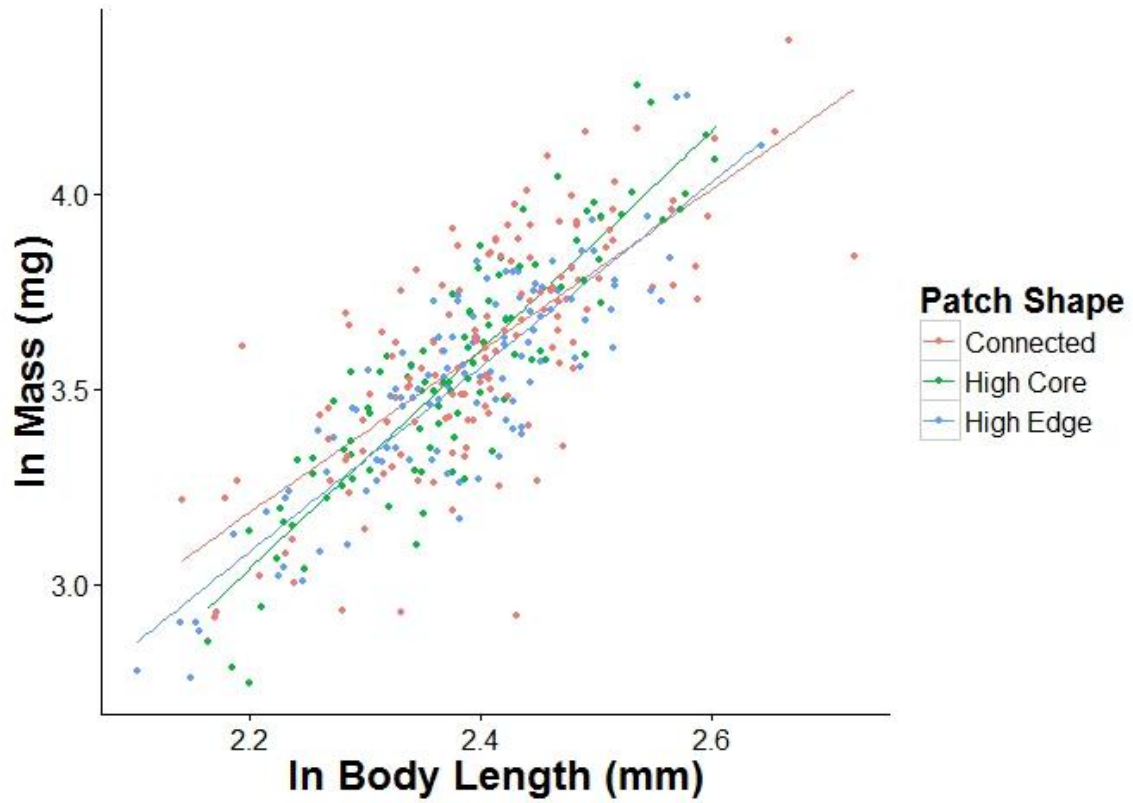


Figure 2-4. Spider allometry by fragment shape. Fragment shape did not alter the relationship between mass and body length.

## **CHAPTER 3: The effect of landscape connectivity on the fitness of reproductive spiders**

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### **INTRODUCTION**

Habitat fragmentation, including isolation of habitats after the loss of habitat, is one of the largest anthropomorphic causes of species extinction (Martinson and Fagan 2014; Harrison and Bruna 1999; Fahrig and Merriam 1994). A popular strategy for reducing extinction in fragmented landscapes is to create landscape corridors, or linear strips of habitat that connect isolated fragments (Hilty, Lidicker Jr., and Merenlender 2006). While corridors have been found to increase the movement of diverse taxa between fragments, it is still unclear whether they fulfill major conservation goals, such as reducing extinction (Haddad, Bowne, and Cunningham 2003; Hudgens and Haddad 2003; Gilbert, Gonzalez, and Evans-Freke 1998; Gregory and Beier 2014). Scientific progress has been inhibited because it is logistically difficult to assess populations over long enough time and at large enough spatial scales to determine a shift in extinction risk (Gregory and Beier 2014; Gilbert-Norton et al. 2010; Schoener et al. 2003). Here, I measure key aspects of life-history to assess if corridors affect a component of fitness that underlies extinction risk.

A key component of fitness is the ability to acquire and store energy and resource allocation represents an alternative indicator of overall success of conservation (Winemiller 2005; Winkler and Wallin 1987). Life-history models assume that energy resources are finite

and must be allocated among reproduction, maintenance, and growth (Winemiller 2005; Jensen et al. 2011). These models assume that allocation is consistent within static environment. However, changes in environmental conditions such as those associated with variation in climate, food availability, and latitude will impact life-history, and thus fitness (Jönsson et al. 2009). Ecological factors altered by global environmental change, including habitat loss and fragmentation, may reduce the available food resources for population dynamics, community structure, and life-history traits (Woods, Brown, and Cobb 2009; Ewers and Didham 2006; Parmesan 2006; O'Sullivan, Benton, and Cameron 2013). Resource allocation is thus one key, but poorly studied dimension of understanding the success of conservation.

Resource allocation can be measured with lipid reserves and have been shown to affect fitness across taxa. Hibernating yellow-bellied marmots living in low altitudes had a longer exposure to food and produced more pups per female than those in higher altitudes with a shorter growth season (Woods, Brown, and Cobb 2009). High lipid content in female Mallards improved survival and breeding success (Boos et al. 2002). In pre-breeding and post-hibernation frogs, lipid reserves increased with latitude, suggesting a buffer against more harsh weather conditions. Across species, individuals use lipid stores to endure unfavorable conditions increase survival and/or reproduction (Post and Parkinson 2001; Mayntz et al. 2009; S. Wilder 2011).

In this chapter, I measure fat reserves at critical stages of life-history in a large-scale corridor experiment to assess if corridors specifically improve a component of fitness of female predators. I first discuss below how one major and common environmental change,

the fragmentation and the isolation of habitats, influences the resource allocation with respect to the fat reserves and productivity of a female predator. I accomplish this by focusing on a part of ecosystems that is poorly studied in the context of corridors but that is of particular interest for the tropic level itself and the effects it could exert in conservation, which is on predators.

Predators are experiencing rapid population declines, largely due to habitat fragmentation (Estes et al. 2011; Ripple et al. 2014). Predators generally have higher spatial requirements to gather resources than taxa from lower trophic levels; smaller, isolated habitat fragments offer less space and fewer resources for taxa from higher trophic levels (R. Holt et al. 1999). In addition, because predators are generally more rare than their prey, they are more susceptible to stochastic extinction events, especially in fragmented landscapes where their populations are inherently smaller (R. D. Holt 2010).

Fragmentation can affect predators directly and also indirectly as mediated by changes in their prey. Environmental changes like habitat fragmentation on prey abundances and therefore availability can also affect predator fitness. Increases in both quantity and quality of prey have resulted in improved fitness for predators (Schmidt et al. 2013; Jensen et al. 2011; Resano-Mayor et al. 2014; Mayntz et al. 2005; Barry and Wilder 2013). For example, the lab-raised spider mites fed a mixed species prey diet deposited twice the number of eggs than those on a single-species diet (Schmidt et al. 2015). Further, the Bonelli's eagle, a top predator, fledged more chicks when fed its preferred prey (Resano-Mayor et al. 2014). Prey abundance and quality thus has direct consequences for how predators allocate resources has direct fitness consequences for predators (Ripple et al. 2014).

Across habitats and taxa, wildlife corridors have been used to reduce the extinction caused by habitat fragmentation. This global investment has promoted the conservation strategy that the projected increase of species movement between formally isolated fragments should maintain survival, growth rate, and most importantly, fitness of vulnerable species (Gregory and Beier 2014).

Conservation strategies to increase predator population abundances or viability should increase the quantity or quality of prey. To do this, they must achieve ecological function that goes beyond their initially intended application to increase movement. They must also positively affect fitness. My research focuses on two aspects of fitness that will connect prey and predator dynamics to underlying population mechanisms, including productivity and female fat reserves. Changes in productivity, or clutch size, influence the lifetime fitness of females (Leborgne, Raymond, Pasquet 2005; S. M. Wilder 2013; Woods, Brown, and Cobb 2009). Fat reserves are a limiting nutrient at the top of arthropod food webs (S. M. Wilder et al. 2013) and predators specifically with high lipid content have shown improved reproduction, survival, and growth (Barry and Wilder 2013; Marden and Rollins 1994; S. Wilder 2011). Thus, by comparing the lipid content of pre- and post- reproductive females, I can discern the available energy females have to invest in reproduction and survival (Jönsson et al. 2009). To accomplish my objectives, I test how habitat fragmentation and corridors affect predator fitness. I do this by measuring the fat reserves of female spiders at critical stages of their reproductive cycle and I do so in a large, experimentally created series of landscapes. I hypothesize that corridors increase spider resource acquisition via prey movement, thus I predict females in corridor-connected fragments to have higher lipid

content while gravid and after reproduction. Furthermore, I predict that increased resource acquisition will result in increased clutch sizes.

## **METHODS**

### **Site Description**

I tested the effects of corridors on predator fitness in the Corridor Experiment at the Savannah River Site (SRS), a National Environmental Research Park located in Aiken and Barnwell Counties, South Carolina, USA (33.20N, 81.40W). The upland habitats of the site are comprised of longleaf pine savanna, a habitat native to the southeastern United States, and with a now fragmented distribution due to land degradation and fire suppression (Frost 1993). Much of the landscape has been converted to plantation pine forest (longleaf and loblolly pine). To test my hypotheses, I conducted my research in an experiment with treatments created by restoring longleaf pine savanna fragments. Fragments were created by clearing mature plantation pine forest into 1 hectare habitat clearings, and planting a low density of longleaf pine trees (*Pinus palustris*; Tewksbury et al. 2002). The experiment is further maintained by burning the landscapes with low-intensity prescribed fire every 2-3 years mimicking natural disturbance frequencies (Frost 1993) and through removal of hardwoods. The experiment consists of 8 replicate blocks, each with one central 1 ha fragment surrounded by four peripheral fragments, each 150m from the central patch and oriented in four cardinal directions. One 1 ha peripheral fragment connected to the central fragment by a 150m long x 25m wide corridor. The other three peripheral fragments are unconnected. The unconnected fragments are each the area of the central fragment plus a

corridor (1.375 ha), but they differ in shape, allowing me to test the potential role of corridors that might confound interpretation of their role in connectivity. Different shapes control for edge effects of corridors. High edge fragments have corridor-shaped extensions that do not connect to another fragment, creating a high edge to core ratio without increasing connectivity. Low edge fragments have a low edge-to-core ratio, and test the role of corridors in increasing fragment area. In each experimental block, one isolated treatment is repeated, and the number of blocks with two high edge fragments is equal to the number of blocks with two low edge patches. In analysis, I control the effects of connectivity from edge effects by comparing corridor-connected fragments to the high edge unconnected fragments. All experimental blocks are separated by at least 1.5 km to minimize the chance of dispersal between them.

### **Study Species**

I investigated the effects of fragmentation and the role of corridors on fitness traits and productivity for female *Peucetia viridans* (green lynx), a large cursorial oxyopid spider that inhabits the open fields of our habitat fragments. Green lynx spiders are a model species for this study because they are abundant in our landscapes, and have a well documented life-history (Whitcomb, Hite, and Eason 1966; Turner 1979; Nyffeler 1987; Fink 1986). Furthermore, their primary prey of bees, wasps, and butterflies, have been found to have increased movement through our corridor-connected landscapes (Randall 1982; Nyffeler 1987; Turner 1979; Townsend and Levey 2005; Haddad and Tewksbury 2005). They are generally semelparous (one egg sac per female), but can be opportunistically iteroparous (multiple egg sacs) with increased food resources or loss of an egg sac (Fink 1986;

Whitcomb, Hite, and Eason 1966). They complete one generation per year, develop over eight molts through spring and summer, become reproductively mature in July and August, and create egg sacs in September and October. Adult females guard egg sacs for 6-8 weeks until the clutch balloons in the second instar and die at the first frost (Fink 1986).

### **Collection**

To test effects of habitat fragmentation and corridors on fitness traits and clutch size, I hand-collected green lynx spiders and their egg sacs in October of 2013 and September of 2014 from one Connected, one High Edge, and Low Edge fragment in each block. I sampled at two different time periods each year, early in the reproductive season (September) and late in the reproductive season (October) to test the consistency of connectivity effects on female lipid content. I performed four surveys within six weeks to assume a closed population of no immigration or emigration between surveys (Pollock 1982). I sampled each fragment for 1.5 hours and surveyed the central 75x75m area by beginning at 12.5 m away from the fragment edge, then searching the 75m perimeter of the fragment. I then moved ten meters towards the interior and searched that 65 meter perimeter and repeated until I circled to the fragment center. The spiraling survey allowed me to quickly cover the most area while remaining thorough. Each year, I targeted to collect 10 spiders per fragment, or a total of 240 spiders. After collection, I immediately stored them in a -5C freezer.

### **Fitness Comparison**

I tested for the effects of habitat fragmentation and corridors on fitness by measuring two fitness traits: clutch size and fat reserves at different life-history stages. I measured clutch size by counting the number of eggs and spiderlings per egg sac. I measured maternal

investment by comparing lipid content of adult females while gravid with those that had produced egg sacs. Finally, I measured lipid content in the eggs and spiderlings themselves. To measure lipid content, I first dried spider samples and weighed them to the nearest 0.001 mg. I then measured lipid content gravimetrically using chloroform extraction (S. M. Wilder et al. 2010). I soaked samples in 2ml of chloroform for 24 hours and repeated twice. I then reweighed samples to calculate the difference in mass before and after lipids were extracted by the chloroform.

### **Statistical Analyses**

To determine the effects of connectivity on fitness traits, I used a linear mixed-effects model, with block identity as a random effect and fragment shape as a fixed effect. As the experimental treatment is the patch, I ran the linear mixed effects regression (lmer) using the mean fitness measurement per patch (Bartlett 1947). All analyses were performed in R (R Core Team, 2013).

## **RESULTS**

I collected a total of 702 green lynx spiders and 147 egg sacs across two years and 24 experimental fragments. As our hypotheses focused on reproductive investment, I excluded males from analyses, leaving 621 adult female green lynx spiders. Connectivity had the largest effect on the lipid content for both gravid and post-reproductive spiders.

### **Lipid Content**

The lipid content in adult females differed significantly based on fragment type (see Table 3-1). Spiders from Connected fragments had higher lipid content than those in High

Edge fragments in gravid and post-reproductive females (see Figure 3-1). Spiders from both Connected and High Edge fragments lose about 30% of their lipid content after producing eggs. However, spiders in Connected fragments have significantly higher lipid content, both when gravid as well as after producing an egg sac. Further, lipid content for gravid spiders in Connected patches is not significantly different from post-reproductive spiders in High Edge patches, suggesting that spiders in Connected patches are able to have the same lipid content as spiders that are gravid. Surprisingly, spiders in the Low Edge fragments had no difference in lipid content for gravid or post-reproductive females.

The following year, however, I did not observe an effect of connectivity on female lipid content (see Table 3-2). I did find that lipid content changed significantly by reproductive status, as post-reproductive females had at most half the lipid content of gravid females, regardless of fragment type (see Figure 3-2). These data are limited, however, because I collected only 7 post-reproductive females in 2014.

### **Clutch Size**

I found that connectivity had no effect on clutch size. The number of eggs per egg sac remained consistent through all fragment types ( $F_{2,18} = 0.1705$ ;  $p = 0.9446$ ; see Figure 3-3).

## **DISCUSSION**

My results demonstrate that corridors increase spider fat reserves at critical points in their life-history. Overall, however, the study yielded mixed evidence for corridors improving fitness. The connectivity effects for lipid content were not consistent across years. Further, connectivity had no effect on clutch size. These findings support that connectivity

may increase fitness through increased fat reserves, but more research is necessary to explore more possible traits to allocate resources. This study supplements a growing body of work that corridors have effects beyond movement, but can affect the fitness, genetic diversity, and species richness of focal species (Orrock et al. 2003; Damschen et al. 2006; Weldon 2006)

Spiders in Connected fragments had significantly higher fat reserves while gravid and again after creating egg sacs. The increased lipids can result in higher fitness because they have more fat reserves to allocate to maternal investment and possibly survival (Schmidt et al. 2013). Regardless of whether females allocate fat reserves directly into reproduction or save their energy for their own survival, green lynx spiders in Connected fragments have the potential to increase their fitness.

Connectivity effects varied across seasons. In 2013 there was a strong, positive effect of connectivity on lipid content. In 2014, spider lipid content shifted by reproductive status, but not by fragment type (see Figure 3-2). This is likely because these spiders were collected at an earlier time in the season so that few individuals had created egg sacs (Whitcomb, Hite, and Eason 1966); I only collected 7 individuals with egg sacs across all fragment types in 2014. Gravid females in 2014 followed a similar trend as in 2013, but a high amount of variation in different fragments made those mean differences not significant. It is interesting to note the pattern of lipid content changed temporally; however, it is not clear how this influences spiders. September, when the 2014 spiders were collected, marks a peak in Hymenoptera abundance, the main prey for green lynx spiders (Turner 1979). It is possible

that green lynx spiders that reproduce in these September experience different prey availability than those in October, and thus allocate fat reserves differently. However more work on the direct link between prey availability and maternal investment is be required.

Connectivity had no effect on clutch size. This was our only direct measure of maternal investment, which suggests that female spiders in connected fragments do not allocate their added lipid reserves to reproduction. However, there are other investments females could make that contribute to fitness. There is a trade-off between the number and size of eggs; therefore instead of females making more eggs, they could shift their investment to the quality of eggs. Because I collected egg sacs which were at different development stages, I could not standardize the size-at-birth to accurately compare size differences. Further, spiders could allocate increased fat reserves for their own survival. This has maternal care consequences because green lynx spiders guard their egg sacs, even after the young emerge. Egg sacs that do not have a female protecting them are highly predated by ants, parasitoids, and spider wasps (Fink 1986; Willey and Adler 1989), therefore increased female survival directly impacts spiderling survival.

Finally, spiders with increased fat reserves could have increased maternal investment by potentially producing another egg sac later in the season. While green lynx spiders are semelparous, they are opportunistically iteroparous under conditions of increased resource availability (Morse and Stephens 1996; Whitcomb, Hite, and Eason 1966). Under lab conditions, Whitcomb et al. (1966) found that most females created two egg sacs; however, they did not observe this in the field. Females have created second egg sacs in the field in California and southern Florida, the date of first frost is too soon in northern latitudes to

allow for the female to survive to build and guard eggs. In South Carolina, Willey and Addler (1989) were able to induce a second oviposition by removing the first egg sac, but did not observe second egg sacs from non-manipulated females. Overall, while I did not find an increased maternal investment for spiders in connected fragments, more work is needed to investigate if females improve their fitness in other ways.

Corridors are created to reduce extinction. One way this can be done is by promoting regular access to resources, which is often limited within small and isolated fragments (Ripple et al. 2014; Polis, Anderson, and Holt 1997; R. Holt et al. 1999). Lipid reserves occur after acquiring excess resources, therefore our evidence of high lipid content in predators indicates that corridors can increase prey availability (Crespin and García-Villalta 2013). Previous studies in this experiment have shown that corridors increase the dispersal of bees, butterflies, and wasps, which are all prey of green lynx spiders (Haddad and Tewksbury 2005; Townsend and Levey 2005). Further, Weldon (2005) found that Indigo Buntings had higher weight, survival and number of fledglings in fragmented habitats with higher abundance of preferred prey (Evans et al. 2012).

Predator populations are declining because of habitat fragmentation and prey depletion (Ripple et al. 2014). Increasing food availability via increased prey dispersal can increase predator fitness. For example, adder survival and body condition increased with high vole density (Forsman and Lindell 1997). Largemouth bass population declined after low prey availability, resulting in low fat content and survival for young fish (Wicker and Johnson 1987). Brown et al. (Chapter 2) found that green lynx spiders receive increased prey from corridor-connected fragments, suggesting that the increased lipid content results from

prey subsidies from the corridor. Because fat reserves from spiders in Connected fragments are higher both before and after reproduction, these spiders are likely more robust to withstand harsh conditions, increase reproduction, and/or have better survival because they have more fat reserves to allocate. This study shows that corridors can make predators, some of the most vulnerable taxa, increase components of their fitness, a critical outcome for conservation.

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Table 3-1. ANOVA table linear mixed effects model of mean lipid content by fragment shape and reproductive status in 2013.

<b>Factor</b>	<b>df<sub>n</sub></b>	<b>df<sub>d</sub></b>	<b>F value</b>	<b>P value</b>
<b>Fragment Shape</b>	2	37	4.1879	0.0229*
<b>Reproductive Status</b>	1	37	2.6296	0.1134
<b>Frag. Shape*Repro Status</b>	2	37	0.9978	0.3784

Table 3-2. ANOVA table for linear mixed effects model for mean lipid content in 2014.

<b>Factor</b>	<b>df<sub>n</sub></b>	<b>df<sub>d</sub></b>	<b>F value</b>	<b>P value</b>
<b>Fragment Shape</b>	2	30	0.8949	0.4193
<b>Reproductive Status</b>	1	30	24.0214	<0.0001*
<b>Frag. Shape*Repro Status</b>	2	30	1.3708	0.2694

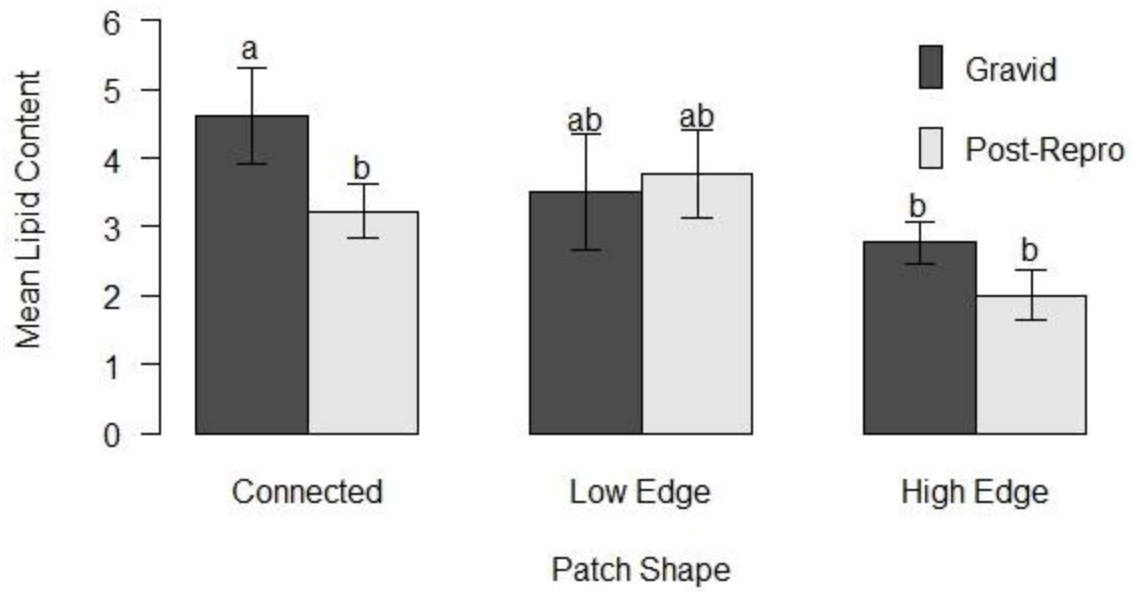


Figure 3-1. Mean lipid content by fragment shape and reproductive status in 2013.

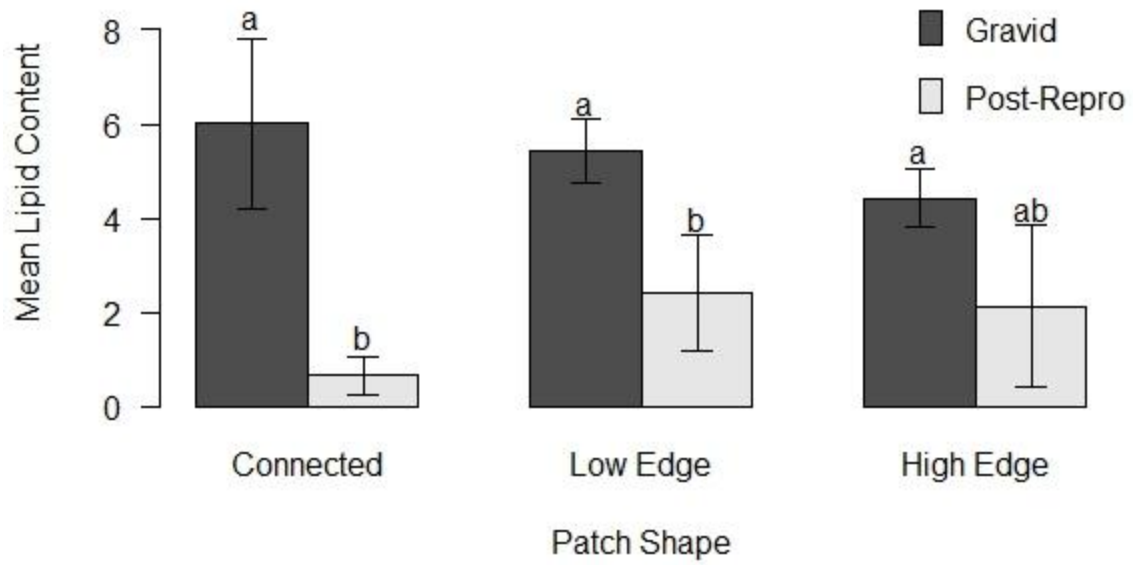


Figure 3-2. Mean lipid content by fragment shape and reproductive status in 2014.

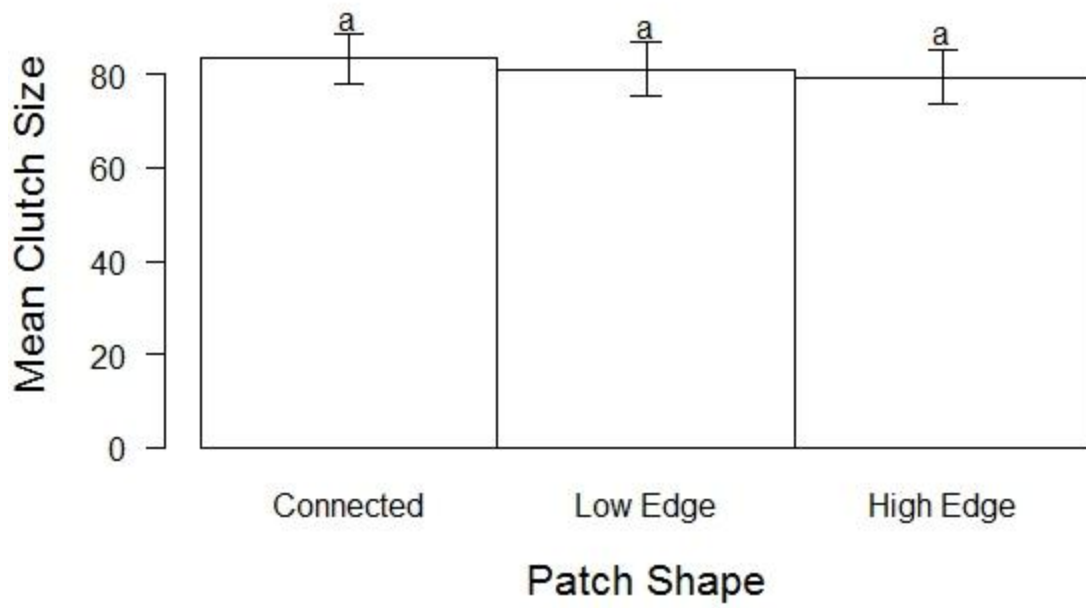


Figure 3-3. Mean clutch size by fragment shape.