REVISITING MESOPREDATOR RELEASE:
CARNIVORE DYNAMICS ALONG A GRADIENT OF LANDSCAPE DISTURBANCE

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by
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ABSTRACT

Human induced habitat loss and predator persecution caused severe declines in apex carnivores throughout the North American continent. Removal of apex predators allowed smaller, lower rank predators from the Order Carnivora to become prominent. These "mesopredators" flourished, destabilizing ecosystems by driving many prey species toward extinction. However, some suggest that mesopredators still benefit from contemporary vegetation changes and fragmentation by thriving in disturbed areas. Many worry the versatility of these mesopredators could further threaten their prey species by leading to increased predation in anthropogenically-disturbed areas. This study seasonally sampled predator distributions along land cover gradients in forested, riparian corridors in Appalachia to identify whether landscape modification results in changes in carnivore community structure in the region. The study area consisted of randomly generated sites along streams in central Pennsylvania. I gathered data from camera traps and field surveys to catalogue the spatial ecology of mesopredators. I analyzed these data with landscape metrics to test the hypothesis that as forest contiguity decreases, both the abundance and richness of the predator community increases, possibly adding pressure on vulnerable prey populations. Through the analysis of these habitat metrics and carnivore occurrence data, this study found that carnivore species richness and abundance do generally increase with human disturbance in rural settings. However, this pattern is not due to the behavior of every species as many mesopredators are present across these rural landscapes and exhibit different responses to disturbance. Nevertheless, a few important generalists, namely the canids and raccoons, do show preferences toward more human disturbed areas and thus, are most accountable for this observed pattern.

Keywords: spatial ecology, mesopredator, predation, forest decline, landscape gradients, riparian corridors, Appalachia, ecological cascades, landscape ecology
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Chapter 1

The Rise of the Mesopredator

“Great and terrible flesh eating beasts have always shared landscape with humans. They were part of the ecological matrix within which *Homo sapiens* evolved. They were part of the psychological context in which our sense of identity as a species arose. They were part of the spiritual systems that we invented for coping... [Today,] every additional child [exerts] additional pressure on the productivity of landscape, turning forests into crop fields and rivers into gutters. Under pressure of this kind, alpha predators face elimination... The foreseeable outcome is that in the year 2150, when human population peaks at around eleven billion, alpha predators will have ceased to exist -- except behind chain-link fencing, high-strength glass, and steel bars.”

- Selected excerpt from *Monster of God* by David Quammen (2004)

The global decline of the charismatic top predator, or apex predator, is a dramatic trend, both in terms of its psychological impact on the human condition and the ecological ramifications it exacts on ecosystems worldwide. Namely, the extirpation of apex predators has been implicated in a long list of ecological cascades, particularly those associated with the degradation of trophic systems (Estes et al. 2011). One of these cascading effects is the "release" of the medium-sized predator, or mesopredator, as is outlined in the mesopredator release hypothesis (Crooks and Soulé 1999). Evidence for this proposed causal link includes observations of competition between these two groups and direct predation stress on mesopredators from their apex relatives (Prugh et al. 2009). These observations span the response of mesopredators to both the extirpation of their apex cousins and the subsequent human reintroduction of top carnivores in select ecosystems (Prugh et al. 2009). Trophic cascades themselves have frequently been the topic of scientific study and ecological literature (e.g., Terborgh and Estes 2010, Eisenberg 2010). This includes the mesopredator release hypothesis. However, rarely does a scientific study take a more holistic view of the processes involved in mesopredator release and as such, a full review of these
processes is long overdue. A few exceptions to this trend can be found in two articles recently published in BioScience: The Rise of the Mesopredator and The Ecological Role of the Mesocarnivore (Prugh et al. 2009, Roemer et al. 2009, respectively). Nevertheless, even these articles fall short of proportionately addressing an important, perhaps the most important, factor: human landscape disturbance. The goal for this literature review and the following case study is to address both trophic cascades and landscape disturbance simultaneously to find the leading cause for the continued success of generalist mesopredators, marked by their versatile ability to flourish in a wide array of landscapes. This review is designed to consider the full complexities of this ecological phenomena and to synthesize recent, relevant literature to ascertain the current level of scientific understanding of the mesopredator release hypothesis and the limitations to the scientific consensus, should one exist.

So what is this mesopredator release hypothesis? While the general idea that reducing carnivores can aid lower order species has existed for decades, the credit for the formal creation of the hypothesis lies with Soulé and his colleagues in their work published in Conservation Biology entitled "Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands" (Soulé et al. 1988). In this seminal work, the mesopredator release hypothesis is first mentioned and outlined to occur when large, dominant predators are removed (Soulé et al. 1988). This absence of the controlling top predators causes smaller predators (often omnivores) to experience population explosions (Soulé et al. 1988). Soulé and colleagues go on to implicate this phenomena in the population declines of particular prey species and imply that this pattern may be widely occurring (Soulé et al. 1988). More than a decade later, Crooks and Soulé (1999) had perfected this hypothesis and continued to provide evidence to validate its controversial premise while continuing to argue for its widespread acceptance. For the past two decades, this ecological concept has garnered significant support, solicited hefty criticism, and been identified as the causal explanation for the downgrading of many ecosystems (Estes et al.
The descriptions of the theory are numerous but most have a singular theme: the removal of large, apex predators leads to the rise and dominance of mesopredators that negatively impact ecosystems (Prugh et al. 2009).

The expansion of the role of the mesopredator has been incriminated in the deterioration of ecosystem resources, mainly witnessed in the population declines of certain prey species (Prugh et al. 2009). This downturn in prey populations has been witnessed is a variety of taxonomic groups including: avifauna (Conner et al. 2010), herpetofauna (Bonnuad et al. 2011), and small mammalian fauna (Eagan et al. 2011). To add complexity, this decline in smaller prey groups is sometimes associated with the expansion of larger prey species that are released in a system in which apex-predators are absent (Beschta and Ripple 2012). This can further impact primary producers through increased herbivory of select species or plant communities (Beschta and Ripple 2012, Estes et al. 2011). Thus, the trophic cascades can fall in multiple directions. Delving into a few specific instances may be helpful to better highlight the breadth of these impacts. For instance, Soulé and his colleague's work emphasizes the impacts that mesopredators have on the decline of bird and other small vertebrate species (1999). In this system, coyotes (Canis latrans) represent the top predators, and following their decline smaller predator species, such as the striped skunk (Mephitis mephitis), raccoon (Procyon lotor), and the domestic cat (Felis catus), enjoy population explosions (Crooks and Soulé 1999). This has a disastrous effect on small vertebrate species, especially scrub-breeding songbirds, due to the overabundance of specialist avian-predators (Crooks and Soulé 1999). But this is just one example and these effects extend beyond southern California. In Indiana, Eagan and his colleagues examined the effects of mesopredator release on small mammal populations (2011). In this study, researchers found that white-footed mouse (Peromyscus leucopus) populations increase drastically in the absence of raccoons (Procyon lotor) (Eagan II et al. 2011). When raccoons are abundant, the inverse is true (Eagan II et al. 2011).
The effects of mesopredator release can even be felt in oceanic systems. Many shark species are subject to rapid population declines due to human persecution and overfishing (Ferretti et al. 2010). The decline of these top oceanic predators can lead to the release of oceanic mesopredators such as other elasmobranchs and marine mammals (Ferretti et al. 2010). These may, in turn, lead to the suppression of the traditional prey species for these groups, although more study is needed in these oceanic ecosystems before firm conclusions can be drawn (Ferretti et al. 2010). However, in fairness, examples do exist where abundant mesopredators appear to have very little impact on prey species. For instance, in a study conducted by Conner and his colleagues, a very low percentage of nestling mortality for songbirds was due to predation by medium sized mammalian predators (6%) (Conner et al. 2011). Instead, in this Georgia study, the two dominate forces behind nestling mortality were snakes (33%) and fire ants (28%) (*Solenopsis invicta*) (Conner et al. 2011). Thus, while cascading effects are common, they are not always present.

**Mesopredators and Landscape Disturbance**

While substantial evidence exists for these and other observed cascading effects, there are also plenty of instances where this hypothesis is either overly simplistic or invalid (e.g., Levi and Wilmers 2011, Ripple et al. 2013, Roemer et al. 2009). To begin, other causal factors must be examined before apex predator declines can be cited as the leading cause of this mesopredator phenomena. One such consideration is that of human landscape disturbance. Medium-sized generalist carnivores tend to do well in human modified landscapes while larger or specialist carnivores tend to do poorly (Prugh et al. 2009 and Roemer et al. 2009). This is due to the ecological truism that what constitutes suitable habitat (and thereby habitat loss) is species specific (Lindemayer and Fischer 2006). Generalist mesopredator species can use a wide array of
landscapes and can be successful even after extensive human modification (Roemer et al. 2009). Specialist or top predators are more adversely affected by habitat loss and fragmentation (Lindenmayer and Fischer 2006). Prugh et al. (2009) mentioned that habitat fragmentation can create additional resources for mesopredators, such as pet food, garbage, and crops. These resources make human modified landscapes a reliable source of food. The expanded use of human modified environments by generalist carnivores exists in both urban/suburban landscapes (e.g., Crooks 2002, Ordeñana et al. 2010, Prange and Ghert 2011) and agriculturally dominated rural landscapes (e.g., Beasley et al. 2004, Devault et al. 2011).

The trend outlined above introduces an important confounding variable: landscape disturbance. Moderate to high levels of disturbance influence both apex predators and lower order cousins, but in opposing ways. This is not to say that the intermediate disturbance hypothesis should now be introduced into the equation as a causal mechanism (Connell 1979). Especially given the extensive criticism intermediate disturbance has faced in recent years (e.g., Wilkinson 1999 and Fox 2013). In any event, the hypothesis would likely only apply to certain mesopredator communities anyway. The argument made here is rather that landscape disturbance may be the underlying reason that apex-predators disappeared and mesopredators continue to do well. Therefore, the landscape should certainly not be overlooked when discussing the mesopredator release hypothesis. For instance, in one of the studies mentioned above, Crooks (2002) attributes habitat fragmentation as a leading explanatory factor for the presence and abundance of carnivores in habitat patches. Specifically, landscape disturbance affects carnivores disparately based on their body size and habitat specialization (Crooks 2002). This study demonstrates that apex-predators are affected by landscape disturbance in opposing ways to the effects such disturbance has on generalist mesocarnivores and that the decline of these top predators is not necessarily the proximal cause of mesopredator release in all circumstances, as they may be occurring simultaneously as a result of landscape change (Crooks 2002).
Another example demonstrates that some mesopredators may take advantage of carrion in agricultural landscapes. Many medium sized predators are excellent scavengers and may be more efficient at using organic remains in human rural landscapes than larger carnivores or even detritivores (Devault et al. 2011). Thus, the dominance of mesopredators in this case is not necessarily due to the removal of their apex relatives, but more because they are pre-adapted to human modified landscapes. Unfortunately, unlike in Crooks (2002), Devault et al. (2011) or Soulé et al. (1999), landscape disturbance is often mentioned only as a footnote or as a way to frame the study area. Too often, it is ignored in the larger discussion and conclusions and thus, becomes an unrecognized, confounding variable. This represents a failure to take into account the full picture or analyze the full system in lieu of focusing on the causal connection between the decline of top predators and the rise of their lower order cousins.

**The Newfound Mesopredator Community**

A second consideration, one that is often underestimated, is the complexity of the mesopredator community. Mesopredators do not all occupy the same trophic level within ecosystems. Numerous studies have indicated that there is substantial intraguild predation within the predator community that can lead to disparate effects among species (e.g., Litvaitis and Villafuerte 1996, Palomares and Caro 1999, Ritchie and Johnson 2009, Thompson and Gese 2007). This complexity is present particularly among canids (Levi and Wilmers 2011) and in systems where a former mesopredator species may have become the functioning top predator (Russel et al. 2009). Indeed, even Crooks and Soulé’s (1999) work on the effects of mesopredator release deals with predators that, in many systems, would be identified as lower order predators. In another study, one previously mentioned (Prange and Ghert 2004), the environmental differences between rural, suburban, and urban settings in northeastern Illinois led to different
mesopredator community compositions demonstrating that landscape can also have varying
effects on generalist mesopredators. Specifically, the closer the proximity to the city, the greater
the proportion of raccoons (*Procyon lotor*) as compared to the other two study species, the striped
skunk (*Mephitis mephitis*) and the Virginia opossum (*Didelphis virginiana*) (Prange and Ghert
2004).

Perhaps the best example of the complexity of carnivore communities can be seen in a
study published in Ecology that directly critiques the mesopredator release hypothesis by
introducing trophic complexities (Levi and Wilmers 2011). The authors’ particular criticism of
the hypothesis is that it was created to explain systems with only three interacting species: an
apex-predator, a mesopredator, and their prey (Levi and Wilmers 2011). This study in Minnesota
demonstrates that the relationships carnivores have with one another become more complicated in
systems with three or more interacting species such as, in this case, the gray wolf (*Canis lupus*),
the coyote (*Canis latrans*), and the red and gray fox (*Vulpes vulpes* and *Urocyon
cinereoargenteus*) (Levi and Wilmers 2011). In this ecosystem, wolves suppressed coyotes
thereby releasing foxes and medium-sized prey species. This response is due to the dietary
preferences of the three species. The two remaining carnivores in this scenario prefer large (gray
wolf) and small (foxes) prey species. In the absence of wolves, flourishing coyotes suppress foxes
thereby releasing both large and small bodied prey species (Levi and Wilmers 2011). The reason
for these releases lie in the coyote’s dietary preference: medium-sized prey species. In short, this
study demonstrates that the mesopredator release hypothesis may be too simplistic to explain the
broader increases in mesopredators across ecosystems. Rather, it is more a way of explaining
particular trophic interactions or population changes of individual species. Therefore, an
unaltered mesopredator release hypothesis, one that fails to take into account landscape dynamics
and the complexity of predator communities, may prove too simplistic and neglect to include
important underlying factors that influence predator communities and the ecosystems where they inhabit.

A Search for Solutions

Understanding the underlying mechanisms behind this modern rise of mesopredators is critical before seeking to mitigate its effects through policy decisions. However, waiting to have a perfect understanding of the system is obviously not practical and when a reasonable knowledge is attained policy decisions must be made. For the purposes of managing mesopredators, there are only two main policy choices: reintroduce apex-predators to control mesopredator populations and thus, limit mesopredator release or manage mesopredator populations through direct anthropogenic population control measures. In either scenario, the populations of mesopredators are managed, the only difference is who plays the role of top carnivore: humans or traditional apex-predators (Hayward and Somers 2009). However, these management strategies only pertain to native mesopredator species. Introduced predator species may require something else entirely: the complete eradication of the local species population. But that is a different debate and is discussed at length in other literature (e.g., Nogales et al. 2004, Cadotte 2009, Zaunbrecher and Smith 1993). The two former management strategies are not without their limitations though and may not work in every circumstance.

At first glance, the introduction of the original apex-predators seems like the most appropriate and natural option. And this strategy has garnered numerous success stories such as reintroduced gray wolves (Canis lupus) suppressing coyotes (Canis latrans) in the western United States (Smith and Bangs 2009, Levi and Wilmers 2011) or expanding dingo populations (Canis lupus dingo) suppressing red foxes (Vulpes vulpes) in Australia (Dickman, Glen, and Letnic 2009). In addition, the preservation or reintroduction of lions (Panthera leo) may be important to
keep other species populations, such as leopards (*Panthera pardus*), under control (Slotow and Hunter 2009, Quammen 2004). However, it is not without limitations. For instance, in some cases, public opinion is very much against the reintroduction of large predators, as was the case in parts of the western United States following the reintroduction of wolves and still is the case in South Africa with the reintroduction of lions (e.g., Smith and Bangs 2009, Slotow and Hunter 2009). A lack of public support may derail this strategy as human-predator conflicts are not a problem that is easily reconciled. Public opinion aside, the underlying landscape may simply be to disturbed or fragmented to sustain a large apex predator, especially when trying to minimize human-carnivore conflict and overlap. For instance, reintroducing the mountain lion (*Puma concolor*) in Pennsylvania would likely prove unsuccessful due to the lack of sufficient tracts of habitat to encompass the home ranges for multiple individuals of the species (averaging at 100 km² each) (Elbroch and Rinehart 2011, Merrit 1987). This is a result of the mountain lions’ habitat needs and their tendency to avoid open or disturbed landscapes (Elbroch and Rinehart 2011, Merrit 1987). In addition, it is likely that conflicts between these reintroduced apex predators and rural human populations would be numerous and ultimately insurmountable, even in "Nittany Lion Country." In these types of situations, the reintroduction of apex-predators is impractical and therefore, another strategy is needed.

In these instances, humans may need to fill the role of the apex predator. Unfortunately, there is a dearth of rigorous scientific study on this topic and so the feasibility and success of this management strategy remain untested. Nevertheless, there are a few examples of preliminary research into this topic (e.g., Conner et al. 2008, Rosatte 2000). In one example, scientists sought to measure the response of raccoon communities to the direct removal of individuals across landscape gradients in the absence of an apex-predator (Beasley et al. 2013). Contrary to expectations, the raccoons did not recover rapidly after this population control measure. Instead, they were sluggish to recover and after three years, only 40% of patches had experienced a full
recovery (Beasley et al. 2013). More importantly, raccoon populations could not rebound without relying on other, separate raccoon metapopulations to act as sources for new individuals (Beasley et al. 2013). The results suggested that culling may be an effective strategy to reduce certain mesopredator populations, as it did in this case. Ethics should be a key consideration when determining the best appropriate management strategy for controlling predators. The effects that each strategy would have on human populations and livelihood must be taken into account in addition to the ecological impacts it would have on the ecosystem. However, a full discussion of the ethics of these strategies is beyond the scope of this literature review.

**Significance and Further Study**

This literature review has demonstrated that two key variables are often overlooked when studying mesopredator release and its effects: the underlying landscape and the complexity and dynamics of the mesopredator community. Thus, this shows the need for more study of these particular variables in conjunction with the mesopredator release hypothesis. A case study I performed for this master’s thesis project was targeted at adding a small piece to this puzzle, namely how does the mesopredator community behave in central Pennsylvania, in the absence of apex predators, particularly along a gradient of landscape disturbance. The methods, results, and conclusions of this case study will compose the third chapter of this thesis and ground the ecological principles discussed in this review in four field seasons of collected observations. The efficacy of this case study reveals community dynamics of mesopredators and how different predator species respond to landscape change, at least in the Ridge and Valley Ecoregion of central Pennsylvania. However, before a case study can be performed, I must first describe the current mesopredator community in central Pennsylvania, the topic of the second chapter of this
This is the layout of the remainder of this thesis and a description of the topics it will address.

However, before I move on to the next chapter, it is always important to ask, why should we care? Why should better understanding mesopredator release and the subsequent trophic cascades it may cause matter to humanity? Or how can understanding the mesopredator community and landscape change benefit humanity? The short answer is because humanity is a part of the global trophic system and any cascading effects, should they reach a sufficient scale, would have detrimental effects on our quality of life and our ability to survive on a changing planet (Estes et al. 2011). Aside from rationalizing this scientific pursuit through human concerns, we may be uniquely placed to determine which ecosystems and species are in trouble, revitalize and repair those that are faltering, and further preserve biodiversity and ecological stability. Even if one assumes that humanity does not stand to lose anything from the downgrading of trophic systems worldwide (a short-sighted and unsubstantiated assumption), the world may be a far emptier place in the very near future if humanity fails to act. If mesopredators do completely replace their apex cousins, something important will surely be lost whether it be ecological stability, passionate environmentalism, or our very identity. Or to put in another way, again in the words of David Quammen (2004), "children [of future generations] will be startled and excited to learn, if anyone tells them, that once there were lions at large in the very world."
Chapter 2

The Mesopredators of Central Pennsylvania

The rise and dominance of the mesopredator community can be witnessed in most places in the continental United States. Central Pennsylvania is no exception. Mesopredators dominate the predator community in the Ridge and Valley ecoregion. Apex predators, on the other hand, are rare. Specifically of the three to four apex predators originally present in this part of the country, only the Black Bear remains (Prugh et al. 2009). The Eastern Timber Wolf (Canis lycaon), the Wolverine (Gulo gulo), and the Mountain Lion (Puma concolor) have all been extirpated from this portion of the country, at least in terms of a viable population (Merritt 1987, Reid 2006, Elbroch and Rinehart 2011). It is important to note though that the American Black Bear does not function as an apex predator in many cases, as did the other three. Instead, black bears, predominantly frugivores, are unlikely to substantially control the populations of lower order predators. Despite these predator declines, a wide array of mesopredators are currently present in central Pennsylvania (see Table A-1 in Appendix A for full listing). Below I have briefly described the most likely candidate to trigger my cameras and outlined their life history characteristics, behavioral propensities, and ecological placement. For this task, I have used a variety of sources including the most recent online survey reports published by the Pennsylvania Game Commission (Lovallo 2008, Lovallo 2013, Lovallo and Hardisky 2012) that can be found at this web address: http://www.portal.state.pa.us/portal/server.pt/community/trapping/11357.

In addition to the species mentioned below, it is important to note that most rural landscapes also are influenced by two domestic predators, namely domestic cat and dog (Felis catus and Canis lupus familiaris). While their effect on these systems is important and they are
quite common, their life history and ecological characteristics are also familiar, and so they are not described here. In short, I have described the relevant life history characteristics of the mesopredator species most likely to be seen in my study region in the following pages, listed in alphabetical order by genus. I have also highlighted my expectations for occupancy and abundance based on these characteristics. Finally, I have included my own example pictures of each species that I collected during this project.

However, before describing each species it is important to discuss the mesopredator guild as a whole. This grouping of mesopredators is extremely diverse and these species respond differently to disturbance, food availability, and provide predation pressure on each other simultaneously. Certain species have been known to limit the abundance of others. For instance, it has been documented that coyotes selectively limit the abundance of red and gray foxes likely due to a perceived competition pressure (Levi and Wilmers 2011, Elbroch and Rinehart 2011). Nevertheless, distinct relationships are not common among the species in this predator guild, but if present, they are generally multifaceted. In addition, predation of one mesopredator on another is usually rare and does not account for the majority of any species mortality (Elbroch and Rinehart 2011, Merritt 1987). For instance, bobcats have been known to kill fishers while fishers have been known to kill subadult lynx and bobcats (Elbroch and Rinehart 2011). While these relationships are numerous and often tenuous, a graphic food web is often helpful to visualize the complexity of this community (Figure 2-1). In the graphic below, the arrows point in the direction of trophic interaction (i.e., toward the predator) and the style of the arrows demarcate the regularity of this interaction. Dotted arrows demonstrate a very tenuous and rare relationship, faded arrows represent an occasional interaction, and solid arrows represent a more regular and important form of predation. Red arrows further indicate the possibility of predation on the entire mesopredator community. This graphic is based on an assessment of life history characteristics and documented observed interactions (Elbroch and Rinehart 2011). This graphic only represents
predator/prey interactions as competitive influences are often more subtle and difficult to assess. Generally, most of these predators are potential competitors, but because of their versatility, the importance of this competition may be reduced. While this graphic could be discussed at length, I will instead focus on only a few interactions. For instance, both coyotes and domestic dogs (with the help of their human companions) are capable of preying on most of the species in this community (Elbroch and Rinehart 2011). In addition, black bears could theoretically prey on most of these species but usually do not because of their dietary preferences (Elbroch and Rinehart 2011). As far as common predator interactions, raccoons and skunks are periodically preyed upon by multiple different predator species (Elbroch and Rinehart 2011). However, the commonality ends there. The rest of the interactions are rare and tenuous. For instance, red foxes have been known to kill fishers and fishers have been known to kill foxes, but these are rare events (Elbroch and Rinehart 2011). In any event, these predation pressures are probably not what drives habitat selection and interaction in most cases, considering that most of these events are so exceptionally rare. Nevertheless, it is possible that skunks and raccoons maybe limited by the presence of other predators and that foxes maybe limited by the presence of coyotes (Elbroch and Rinehart 2011, Levi and Wilmers 2011). Other than these trends, this food web may not be of much importance. In short, this mesopredator guild is defined by species that sometime prey upon another, but not usually.
Figure 2-1. A representation of the mesopredator community food web. Each circle is a mesopredator species and each arrow represents a predatory interaction pointing in the direction of the acting predator in said interaction. The three levels of shading for the arrows represent how often the interaction occurs, with dotted arrows representing tenuous interactions and darker arrows representing more common interactions. The three predators inside the larger circles with red arrows indicate potential top predators with the capability to influence the entire guild. Humans can influence the entire system as well and often act a control on every other predator.

The complexity of this mesopredator guild distinctly applies to landscape change as well. For instance, Crooks (2002) stated that medium-sized, generalist carnivore species either dramatically benefitted from the isolation and fragmentation of naturally vegetated landscape patches (e.g., gray foxes, opossums, domestic cats) or showed no preference (e.g., raccoons, striped skunks). Other, more specialized, species tended to decline in the wake of landscape fragmentation (e.g., badgers, weasels, spotted skunks, bobcats, coyotes, and mountain lions) (Crooks 2002). The main point here is that “all carnivores are not created equal” and that

- Black Bears
- Gray Foxes
- Opossum
- Coyotes
- Domestic Dogs
- Domestic Cats
- Mink
- Raccoons
- Red Foxes
- Skunks
- Fishers
- Bobcats
- Humans
landscape processes such as fragmentation affect species differently, even those belonging to the same guild (Crooks 2002 p500).

In any regard, because of this complexity, perhaps the best way to describe this guild is to examine the individual species. For a brief summary, consult Table A-2.

**Coyote (Canis latrans)**

The coyote was not always as widespread as it is today and probably first arrived in Pennsylvania during the 1980s (Merritt 1987 and Elbroch and Rinehart 2011). However, today this species is prevalent across all of North America and inhabits just about every environment imaginable (Elbroch and Rinehart 2011). An extremely versatile generalist, coyotes are omnivorous, highly adaptable, and active throughout the year (Elbroch and Rinehart 2011). They are generally crepuscular (though they can be active during the day and night as well) and can cover large distances during a single day (Elbroch and Rinehart 2011). Most importantly, coyotes,
even though common, are extremely elusive and secretive (Merritt 1987). Ironically, while commonly occupying human landscapes, it is rarely seen by people (Merritt 1987, Elbroch and Rinehart 2011). In fact, packs of coyotes have even been known to travel in single file, concealing their numbers (Elbroch and Rinehart 2011). In addition, coyotes can wander large areas, especially as individuals and can move extremely quickly across the landscape (Merritt 1987). Most importantly, it is possible that coyotes may function as apex predators in certain systems (e.g., Levi and Wilmers 2011) but it is unclear if they do so in Pennsylvania. In terms of abundance, the Pennsylvania Game Commission reported an estimated 15,900 coyotes harvested in 2011-2012 season but still maintained that the number of complaints has remained consistent for the past two decades (Lovallo and Hardisky 2012). In addition, 609 coyotes were harvested from the wildlife management unit encompassing my study area in the 2011-2012 season (Lovallo and Hardisky 2012). In short, the Game Commission speculates that coyote populations remain stable throughout most of the state.

Therefore, for this study, I expect coyotes to occupy a large array of habitat types and to be present across the landscape. However, the likelihood of documenting coyotes via invasive survey techniques is extremely remote. Nevertheless, noninvasive methods, such as camera trapping, should lead to an accurate picture of how coyotes use the landscape.
Opossum (*Didelphis virginia*)

Figure 2-3. *Didelphis virginia* at a moderately disturbed site.

Opossums, another common species, are not technically a member of the order Carnivora, but are instead North America’s only native marsupial. Nevertheless, this species does exhibit many of the same ecological characteristics as its mammalian counterparts in the order Carnivora. For instance, like many mesopredators, it is distinctly omnivorous and will eat just about anything, even each other (Elbroch and Rinehart 2011). They are also able to adapt to a wide variety of environmental conditions (Merritt 1987). Opossums are active year round and are distinctly nocturnal for most of the year but this can shift during the winter months (Elbroch and Rinehart 2011). Members of this species do not have distinct home ranges and are highly nomadic moving across the landscape in search of food (Elbroch and Rinehart). Similar to raccoons, opossums prefer habitat in close proximity to streams and other water bodies, especially along forest edges (Merritt 1987). Once again, the Pennsylvania Game Commission recently reported that approximately 49,500 opossums were harvested in the 2011-2012 season.
but did not report on population condition (Lovallo and Hardisky 2012). In addition, approximately 2,100 opossum were harvested from the local wildlife management unit (Lovallo and Hardisky 2012).

Therefore, I also expect this species to be a quite common generalist in many rural and urban settings throughout the year. It is likely that this species will be more common along forest edges and will utilize both cultivated and forested landscapes. However, unlike raccoons, repeat visits by individuals across multiple nights are not likely due to their highly nomadic nature.

**Bobcat (Lynx rufus)**

![Bobcat](image)

Figure 2-4. *Lynx rufus* at a less disturbed, interior forest site.

Bobcats are considered to be specialist predators and unlike other members of the order Carnivora, are exclusively predatory carnivores though carrion is often included as a portion of their diet (Merritt 1987, Elbroch and Rinehart 2011). Their need for habitats with vegetated cover stems mostly from the need for optimal areas to hunt prey (Merritt 1987). Overall, they tend to
remain more isolated from humans than many carnivore species and thus, to prefer more mountainous and forested landscapes in Pennsylvania (Merritt 1987). However, they are capable in living in a variety of habitats but the need for a higher level of habitat quality is fairly constant (Elbroch and Rinehart 2011). In short, bobcats do not usually tolerate significant amounts of habitat disturbance. Bobcats are mainly crepuscular, but can be active at other times of the day and night as well (Elbroch and Rinehart 2011). In addition, bobcats are active and hunt year round though their target prey species can shift depending on prey availability (Elbroch and Rinehart 2011). Like many felids, bobcats are solitary with home ranges that are reasonably large for their size (Merritt 1987). In the bobcat management plan prepared by Lovallo (2013) put forth by the PA Game Commission, bobcat populations are reported to be either stable or increasing in most of Pennsylvania and the species seems to have mostly recovered from previous range contractions and low population numbers. Reported evidence on the population stability is the increasing number of bobcat mortality due to vehicles, more than 100 a year since 2000 (Lovallo 2013). More detail and evidence is available in this extensive report, but bobcats seem to be doing fairly well in Pennsylvania.

In central Pennsylvania, I expect bobcats to occupy ridgelines and areas of intact forest and become less common as human disturbance increases. Therefore, I expect bobcats to exhibit distinct habitat preferences that would be captured with a variety of sample techniques. In addition, repeat visits to sites are not expected, due to their large home range.
Fisher (*Martes pennanti*)

Figure 2-5. *Martes pennanti* at a less disturbed, interior forest site.

Previously extirpated as a result of deforestation and overharvesting, fishers were successfully reintroduced to Pennsylvania (Merritt 1987, Serfass and Dzialak 2010). While the fisher is still considered vulnerable in Pennsylvania, it is present throughout much of the state spreading from its original release sites in north-central Pennsylvania and is once again an important member of the predator community (Steele et al. 2010, Serfass and Dzialak 2010). The fisher is a habitat specialist preferring large isolated, tracts of forest (Merritt 1987). They are considered arboreal, able to forage throughout vertical strata of the forest. In addition, they tend to avoid crossing large open areas and prefer woodlands with vegetated cover close to the ground (Elbroch and Rinehart 2011). Members of this species are flexible hunters and can switch prey species based on food availability, but their prey usually consists of small to medium-sized mammals (Elbroch and Rinehart 2011). Fishers are active year round and are neither nocturnal nor diurnal though their activity levels usually peak during crepuscular hours (Elbroch and
Rinehart 2011). They also have large home ranges but often visit the same locations multiple times looking for food (Elbroch and Rinehart 2011). According to the PA Game Commission and Lovallo (2008) in the Fisher management plan, fisher are rapidly expanding throughout portions of the state. This is evidenced by an increasing number of road mortalities and observations (up to 511 in 2007). Nevertheless, the species is still not well established in portions of the state and remains rare (Lovallo 2008).

In short, this rare species is expected to be quite rare in Pennsylvania and will likely only be found in or near its optimal habitat conditions: intact and contiguous forest. In addition, if a fisher is seen twice in the same location, it is quite likely to be the same individual.

**Striped Skunk (Mephitis mephitis)**

![Striped Skunk](image)

Figure 2-6. *Mephitis mephitis* at a highly disturbed, agricultural site.

Another common and well known generalist carnivore in Pennsylvania is the striped skunk. Striped skunks are adaptable and can be found in many different environments across the
United States (Merritt 1987, Elbroch and Rinehart 2011). This species is most abundant around human developments and along edge habitats (Elbroch and Rinehart 2011). Contrastingly, they are not usually found in dense forest stands (Merritt 1987). Skunks are true omnivores and will eat a wide array of foods, especially refuse (Elbroch and Rinehart 2011). Members of this species are usually active at night throughout most of the year (Merritt 1987). However, skunks will endure periods of winter torpor, living off fat stores when weather conditions are especially harsh (Merritt 1987, Elbroch and Rinehart 2011). Interestingly, skunks are not generally found near water despite their versatility and adaptability (Merritt 1987). In the 2011–2012 season the PA Game Commission reported that approximately 13,000 striped skunks were harvested, the most in more than a decade (Lovallo and Hardisky 2012). About 1,500 were harvested from the wildlife management unit encompassing my study area (Lovallo and Hardisky 2012).

In short, skunks are expected to be present in a variety of habitats, and show a clear preference toward human occupied landscapes. In addition, their abundance would be expected to decline in the colder winter months.
Mink (*Neovison vison*)

Figure 2-7. *Neovison vison* at a less disturbed, interior forest site.

A perfect example of a specialist carnivore, mink inhabit forested riparian or wetland zones and spend almost all of their lives within a short distance from the water’s edge (Merritt 1987, Serfass and Brooks 1998). Though this species is widespread throughout Pennsylvania, it is usually found in particular habitats associated with the banks of streams and lakes (Merritt 1987). In addition to these specialized habitat preferences, mink also specialize in small mammals and aquatic prey such as fish and herpetiles (Merritt 1987). However, like most mesopredators, mink are flexible and can modify these preferences based on food availability (Elbroch and Rinehart 2011). It is generally a nocturnal species, but can have higher amounts of activity around dusk and dawn (Merritt 1987). According to the PA Game Commission, approximately 12,000 mink were harvested in the 2011-2012 season, including 567 from the wildlife management unit encompassing my study region (Lovallo and Hardisky 2012). This harvest number is much higher than the past few years but seems consistent with previous older harvests.
While this species does have particular habitat preferences, it can generally be found anywhere near water and where there is an adequate food source. Thus, mink are expected to range widely but to prefer riparian zones of a higher stream habitat quality due to their aquatic hunting needs.

**Raccoons (Procyon lotor)**

![Figure 2-8. Procyon lotor at a less disturbed, interior forest site.]

An extremely prevalent species in most of the continental United States, raccoons are versatile generalists that can occupy a wide range of environmental conditions (Elbroch and Rinehart 2011) but are reported to prefer vegetated areas close to water, particularly streams (Merritt 1987, Elbroch and Rinehart 2011). More importantly, for the course of this study, raccoons have been identified as a facultative wetland species, meaning that they use wetland areas heavily (Serfass and Brooks 1998). Thus, this species will likely be quite abundant in any sampling technique targeted around riparian corridors, such as this thesis project. In addition,
raccoons are one of the few species that actually increases in abundance as human development increases (Elbroch and Rinehart 2011). From a dietary perspective, raccoons are also generalists being highly omnivorous and able to adapt to a variety of food sources (Merritt 1987). Raccoons are nocturnal, non-territorial, and have home ranges of widely variable sizes (Elbroch and Rinehart 2011). However, a raccoon’s movements center mostly around food and water availability (Elbroch and Rinehart 2011). Finally, raccoons are active in all four seasons, but will remain in a den during especially cold periods in winter (Merritt 1987). As far estimating population, almost 175,000 raccoons were harvested in the 2011-2012 season, as estimated by the PA Game Commission (Lovallo and Hardisky 2012). In the local wildlife management unit, more than 6,000 were harvested (Lovallo and Hardisky 2012). This harvest is far greater than those of the past decade and is consistent with the largest counts in recent history.

Based on these characteristics and for the purposes of this study, raccoons can be considered a quintessential generalist, expected to occupy a many different habitat types, but to increase in abundance and prevalence as human disturbance increases, as long as food and water is available. However, it is possible that their abundance would lessen in the colder winter months. In addition, they are quite likely to be repeat visitors to sample sites, often in groups, and to remain at the sites as long as food is present.
Gray Fox (*Urocyon cinereoargenteus*)

![Gray Fox](image)

Figure 2-9. *Urocyon cinereoargenteus* at a highly disturbed site.

An unusual arboreal canid, gray foxes are forest dwellers that can rotate their forelimbs to assist with climbing trees (Elbroch and Rinehart 2011). This arboreal specialization is also a limiting factor as the species seldom occupies nonforested areas, where vegetated cover is minimal (Elbroch and Rinehart 2011). If the species is present in an area, however, they are usually relatively common (Elbroch and Rinehart 2011). In Pennsylvania, this species shows a distinct preference toward deciduous forest, but will use other, more open habitats at times (Merritt 1987). However, this species is generally regarded as less tolerant of human development than some of its other canid relatives (Merritt 1987). These foxes are the most omnivorous of the canids, both hunting a variety of small prey and simultaneously foraging for mast (Elbroch and Rinehart 2011). However, these dietary preferences do change based on the season and are thus quite versatile generalists in terms of diet (Merritt 1987). This species is also active year round and mostly nocturnal, once again with peak activity levels around dawn and dusk (Merritt 1987).
According to the Pennsylvania Game Commission, approximately 19,000 gray foxes were harvested in the 2011-2012 season, a number lower than most previous recorded years (Lovallo and Hardisky 2012). Around 1,400 of those harvests occurred in the same wildlife management unit of my study location (Lovallo and Hardisky 2012). However, there does not appear to be any consistent decline in gray fox harvest numbers.

In short, this species would be expected to occupy forested and possibly forested edge areas while attempting to stay somewhat removed from human presence. They would also be expected to be found in every season and to use more open habitats when necessary.

**Black Bear (Ursus americanus)**

![Black Bear](image)

Figure 2-10. *Ursus americanus* at a moderately disturbed, forest-edge site.

While not strictly a mesopredator, black bears are an important component of the predator guild in Pennsylvania. However, black bears are actually not as predatory as many of the other carnivores previously mentioned. In fact, they are as much herbivores as they are carnivores
and will eat only small amounts of meat depending on the time of year (Elbroch and Rinehart 2011). In many cases, black bears are predominantly frugivore, eating fruits and nuts for the majority of their diet (Merritt 1987). Formerly, widespread throughout the continent including the eastern United States, they now mostly reside in forested mountainous regions (e.g., the Appalachians) (Elbroch and Rinehart 2011). In Pennsylvania, these bears prefer to live in heavily forested areas that are inaccessible to humans (Merritt 1987). Though, in areas with higher densities, black bears will use agricultural and suburban portions of the landscape. However, as is the case for most carnivores, these choices are predominantly driven by food availability (Merritt 1987). Bears are active throughout the year, save the winter months when they hibernate (Merritt 1987). Like many of the previously mentioned species, black bears have also been expanding in range and population according to the PA Game Commission and now appear more frequently in some counties and wildlife management units (Lovallo and Hardisky 2012). Once again, the mortality due to vehicles and the annual harvest counts have increased in recent decades, culminating in more than 4,000 bears being harvested in 2005 (Lovallo and Hardisky 2012).

Based on these observations, I expect black bears to be present in many forested areas of Pennsylvania, but to generally avoid those areas with a distinct human presence. In addition, these predators would not likely be observed active during winter months.
Red Fox (*Vulpes vulpes*)

Figure 2-11. *Vulpes vulpes* at a highly disturbed, agricultural site.

This species, at least in Pennsylvania, is likely descended from the European red fox introduced in portions of the eastern United States (Merritt 1987). As opposed to their smaller, arboreal cousins, red foxes generally prefer more open and disturbed habitats and exist in closer proximity to human civilization (Elbroch and Rinehart 2011). While generally an extremely adaptable species and quite widespread, foxes in Pennsylvania may be more selective in terms of habitat than in other regions (Merritt 1987). Red foxes generally avoid forested areas and thrive in human modified landscapes, close to adequate water sources (Merritt 1987). Thus, agricultural fields or pastures could be considered prime habitats for this species (Merritt 1987). As far as dietary preferences, red foxes also are omnivores though their diet consists of mostly small mammals and they are quite adept hunters (Elbroch and Rinehart 2011). Similar to their gray cousins, these foxes are active year round and are generally nocturnal with primary activity during crepuscular hours (Elbroch and Rinehart 2011). According to the PA Game Commission,
more than 68,000 red foxes were harvested in the 2011-2012 season (Lovallo and Hardisky 2012). This number is more than double the average for the previous decade and a clear pattern of increasing harvest counts is evident. However, only 1,300 of those harvests were from the wildlife management unit encompassing my study area (Lovallo and Hardisky 2012).

Therefore, this species is expected to occupy the edges of forests and human modified portions of the landscape and be quite common throughout the year.

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As is evident in these numerous descriptions, these species have disparate habitat needs, dietary preferences, and population statuses here in central Pennsylvania. Unfortunately, a precise population estimate is expensive and difficult to acquire and so the PA Game Commission mostly relies on more indirect metrics for these species such as the previously mentioned harvest counts or recorded road mortalities. Nevertheless, these measures demonstrate that the majority of species in this community appear to be either stable or expanding and that they are likely be present in this study region. In short, mesopredators appear to be established and continually expanding, with a few species strongly dominant in terms of frequency, at least in central Pennsylvania. The following case study will help to validate these documented life history characteristics and indirect abundance and density measures in addition to addressing how these many species use a gradient of landscape disturbance.
Chapter 3

Case Study: Mesopredator Community Dynamics along a Gradient of Landscape Disturbance in Central Pennsylvania

In ecosystems where apex predators are absent, how do mesopredators interact and use an increasingly human landscape? This is the key question this case study seeks to address. This study strives to quantify elements of the two confounding variables in other mesopredator studies: the behavior of the mesopredator community and the impact of landscape patterns on that community. My master's thesis project addresses the impacts of anthropogenic land-use, in the Ridge and Valley Province of the central Appalachians of Pennsylvania, on the population and community dynamics of these previously described mesopredators, sometimes referred to as mesocarnivores. Specifically, this project focuses on the impact of a gradient of declining natural vegetation, which is mostly deciduous forest in this region, along stream corridor networks (i.e., habitat loss or fragmentation). Past research has attributed mesocarnivore presence and expansion to decreased forest cover (although not necessarily in this region or along corridor networks), but usually has not included the analysis of the entirety of the mesopredator community. In short, this study utilizes principles from landscape ecology, spatial ecology, and biogeography to analyze the population dynamics and distribution of the mesopredators in the targeted study region.

Landscape Change and Corridors

Forest cover decline remains a large problem in much of the world, especially developing countries (Drummond and Loveland 2010). The eastern United States is not immune to this problem. During much of the 20th century forest cover was expanding due to abandonment and
subsequent regrowth of woody vegetation on agricultural lands. This trend, however, has reversed during the latter portion of the century (Drummond and Loveland 2010). For instance, the Ridge and Valley ecoregion had a decline of forest cover throughout the past three decades, losing 1.5% of its forest cover over this portion of the study period (Drummond and Loveland 2010). This number might be misleading low. In another study, researchers found that a 1.1% forest cover net loss translated to much greater net losses of the interior forest, possibly upwards of 10%, when taking into account forest fragmentation (Riiters and Wickham 2012). Specifically in some areas of Pennsylvania, increased forest fragmentation was evident only when examining smaller landscape patches at finer scales (Bishop 2008). When examining forested land cover trends using larger patch size or coarser scales, minimal land cover change was evident (Bishop 2008). These discrepancies are due, in part, to the difference between overall forest loss and fragmentation as well as differences in scale. For instance, many areas could be subject to small amounts of overall forest loss, but large amounts of forest fragmentation if small, targeted tracts of deforestation isolate existing forest and serve to expose forest interiors (Riiters and Wickham 2012). Practically, interior forest loss may be a more important measure of habitat for many species due to edge effects and specific species' habitat requirements (Lindenmayer and Fisher 2006). This is because some species simply cannot use the edge of forests in the same way that they can use interior forest for a variety of climatic and ecological reasons (Lindenmayer and Fisher 2006). For instance, edge habitats may lead to both increased predation from various edge-loving species and harsher temperature drops in winter, leading to increased mortality for some species. Due to this pattern, forest fragmentation can have similar negative effects to overall forest loss and can lead to outright habitat loss (Lindenmayer and Fisher 2006). Thus, forest cover loss and fragmentation is a relevant conservation concern in the eastern United States and the Mid-Atlantic region.
The loss, subdivision, or degradation of forest cover in any form is associated with the loss, subdivision, or degradation of habitat for a variety of species (Lindenmayer and Fisher 2006). However, this is not always the case as what can be considered suitable habitat is, by definition, species-specific (Morrison et al. 1992, Lindenmayer and Fisher 2006). Because of this, what constitutes habitat loss is also specific to a species (Lindenmayer and Fisher 2006). As discussed in the previous chapter, forest cover decline and other landscape changes affect mesopredators differentially. But since generally, "mesopredator outbreaks are commonly observed in fragmented habitats" meaning that this group tends to thrive in heavily modified habitat (Prugh et al. 2009), fragmented landscapes in rural areas are excellent study regions for this phenomena. In short, fragmented systems that also contain corridors facilitating movement within the fragmentation provide the perfect landscapes to study the mesopredator community.

In addition, the effects of landscape disturbance and habitat loss are common along narrow forest corridors, where even small amounts of forest loss or decline can greatly reduce the usable habitat for selected species (Lindermayer and Fisher 2006). Landscape corridors themselves are important and a key part of the Patch-Matrix-Corridor Model in landscape ecology (Lindermayer and Fisher 2006). Specifically, this model described by Forman (1995) defined corridors as strips of a particular land cover type that are different from the surrounding landscape on either side and connect other habitat patches.

Particularly, these corridors can act as ecological or conservation corridors, physically linking patches of native vegetation and thereby aiding both the movement of wildlife through a suboptimal matrix while simultaneously providing habitat where select species may reside. In this model and particularly along corridors, edge effects are important as they can have a variety of effects on species behavior and ecosystem stability, including the utility of a given corridor for a particular species. This patch-matrix-corridor model has been widely adopted in conservation
biology and is used by policy makers to manage habitat for a variety of wildlife species (Lindermayer and Fisher 2006).

I chose riparian corridors as the study sites for this project because of their suitability for mesocarnivores. In addition, riparian zones often account for the last remnants of forested habitat in a region subject to rural and urban development. The narrowing and fragmentation of these corridors is critical as riparian zones provide excellent habitat for a variety of species and pathways for wildlife to move between remnant habitat patches (Brooks 2013). Particularly, the patterns that develop along riparian corridors influence both the function and structure of these ecosystems, impacting the integrity of their biological communities (Brooks 2013). For that matter, the same is true of the neighboring terrestrial ecosystems that depend on the corridor and habitat it provides. Ultimately, the quality of the corridor must be assessed by examining measures such as percent forest cover and corridor width. Width is exceptionally important as the corridor must "be sufficiently wide to maintain suitable interior conditions" while taking into account edge effects such as "changing microclimates, increased predation, and parasitism" (Brooks 2013 p469). These riparian corridors are important to many wildlife guilds, including birds and mammals (Croonquist and Brooks 1993). Particularly they provide habitat for waterfowl, shorebirds, and "semiaquatic mammals such as muskrat (Ondatra zibethicus), mink (Neovison vison), raccoon (Procyon lotor), and river otter (Lontra canadensis)" (Brooks 2013 p467). However, even though they are often the last natural remnants in disturbed landscapes, these corridors are by no means immune to human disturbance. But thankfully, as Allan (2004 p258) states, "investigators increasingly recognize that human actions at the landscape scale are a principal threat to the ecological integrity of river ecosystems". For instance, in another study of 16 streams in eastern North America, riparian areas are not immune to deforestation pressures and that this deforestation "not only reduces wildlife habitat and corridors but also directly
impacts the stream itself” (Sweeney et al. 2004 p14132). Thus, riparian corridors provide fitting
study sites to study connectivity for wildlife and landscape change, particularly for wildlife
species. They also provide a natural center point to measure landscape change and perform a
variety of landscape analyses.

The concept of corridors as homogeneous landscape structures that provide simple paths
from one landscape patch to another is misleading. This view largely ignores spatial complexity
such as landscape gradients and the fact that a single classification of habitat may not be
appropriate for more than one species (Lindenmayer and Fisher 2006). This limitation suggests
the importance of ecosystem gradients particularly in regard to forest cover and other land cover
classifications. Allan (2004 p258), stresses that rivers particularly are "complex mosaics of
habitat types and environmental gradients, characterized by high connectivity and spatial
complexity." This is vital to many species, particularly semiaquatic species such as amphibians as
they "require both terrestrial and aquatic habitats and various times in their life cycles" (Brooks
2013 p466). In short, "river and streams are often seen as the epitome of connectivity" but "there
is [also] a rich texture of spatial heterogeneity both within streams and river and in the
surrounding terrestrial landscape" (Wiens 2002 p507). Thus, riparian corridors are excellent
systems to study, particularly when examining forest cover decline, landscape gradients and
wildlife activities. They provide habitat and corridors for wildlife, provide a finer scale to view
forest cover gradients, and are extremely susceptible to deforestation and forest degradation. It is
for these reasons that riparian corridors provide excellent study sites to analyze the gradient of
human landscape disturbance that exists in the Ridge and Valley Ecoregion and its impact on
mesopredator expansion.
Study Objectives

The main goal of this study was to determine landscape factors that influence the structure and characteristics of the mesopredator community in the absence of apex predators. Central Pennsylvania, with its dearth of top predators, provides an excellent study location to answer this question. With this overall goal in mind, my main research questions were as follows:

1. How are mesopredators impacted by human landscape disturbance?
   A. Is the presence or absence of mesopredators associated with landscape disturbance?
      i. Null Hypothesis: The presence or absence of mesopredators is not associated with landscape disturbance.
      ii. Alternative Hypothesis: The presence or absence of mesopredators is associated with landscape disturbance. I expect moderate levels of landscape disturbance to be associated with increased carnivore occurrence.
   B. Is the relative abundance of mesopredators associated with landscape disturbance?
      i. Null Hypothesis: The relative abundance of mesopredators is not associated with landscape disturbance.
      ii. Alternative Hypothesis: The relative abundance of mesopredators is associated with landscape disturbance. I expect moderate levels of landscape disturbance to be associated with increased carnivore abundance.

2. Do these responses differ among the different mesopredator species, particularly based on like taxonomic or ecological groups?
A. Are taxonomic differences associated with the response of mesopredators to disturbance? (e.g., Canids vs. Felids)
   i. Null Hypothesis: Different taxonomic groups respond to landscape disturbance in similar ways.
   ii. Alternative Hypothesis: Different taxonomic groups respond to landscape disturbance in different ways. I expect the more omnivorous taxonomic group Canidae to be more associated with disturbed habitats.

B. Are ecological or species differences associated with the response of mesopredators to disturbance? (e.g., generalists vs. specialists)
   i. Null Hypothesis: Ecological differences do not seem to influence how mesopredators respond to disturbance.
   ii. Alternative Hypothesis: Ecological differences appear to influence how mesopredators respond to disturbance. I expect generalist mesopredators, such as Canis latrans, Vulpes vulpes, Procyon lotor, and Didelphis virginiana, to be most abundant in moderately disturbed habitats and specialist mesopredators, such as Lynx rufus, Neovison vison, and Martes pennant to prefer minimally disturbed habitats.

3. Are these responses associated with other environmental variables or the responses of other species?
   A. Does the manner that mesopredators occur and respond to disturbance differ temporally?
      i. Null Hypothesis: The mesopredator community’s responses to landscape disturbance does not vary temporally.
ii. Alternative Hypothesis: The mesopredator community’s responses to landscape disturbance does vary temporally, at least for certain species or groups.

B. Does the manner that mesopredators occur and respond to disturbance differ seasonally?

   i. Null Hypothesis: The mesopredator community does not experience seasonal variation.
   
   ii. Alternative Hypothesis: Seasonal differences are associated with differences in the structure of the mesopredator community and its response to landscape disturbance. I expect generalist predators to shift their distributions more into agricultural lands in the summer and fall seasons and more into forested lands in the spring and winter seasons, likely due to increased food availability during peak agricultural seasons.

C. Is the manner that some mesopredators respond to disturbance associated with the response of other predators in the same guild?

   i. Null Hypothesis: The responses of predator species do not seem to depend on the responses of fellow predators in their own guild.
   
   ii. Alternative Hypothesis: The responses of at least one predator species appear to depend on or be associated with the responses of another predator species. I expect the abundance of larger predator species to be negatively associated with the abundance of smaller carnivores.

4. Which characteristic(s) of human landscape disturbance appear(s) to most influence the mesopredator community? (e.g., microclimatic variations, vegetative cover loss, increased human presence, etc.)
i. Null Hypothesis: No particular characteristics can be separated as more influential than the others.

ii. Alternative Hypothesis: At least one characteristic can be highlighted as more influential on the mesopredator community than the others. I expect both the loss of vegetated cover and increased food availability to be the most important factors influencing the presence and abundance of mesopredators.

In short, my expectations for this project are to quantify and analyze the response of mesopredators to increasing levels of human landscape disturbance. For the purposes of this study, human landscape disturbance was defined as the loss of natural, woody vegetation due to human land use practices. I hypothesize that as this human disturbance increases, so too will generalist mesopredator species richness, relative abundance, and daily activity. In extremely disturbed habitats, I think these trends will be reversed. In regards to specialist mesopredator species, I hypothesize that their occurrence and abundance will rapidly decline with increased human land use. As a result of these two opposing trends, I expect moderately disturbed habitats, located along landscape patch edges, to contain the largest assemblages of carnivores and the most carnivore activity. This is in line with the intermediate disturbance hypothesis discussed previously.

**Study Area**

The study area of this project was confined to the Mid-Atlantic Region of the U.S. and concentrated within the central Ridge and Valley Province of Pennsylvania. More specifically,
the study sites were composed of two riparian zones already under observation by Riparia located in the Shaver's Creek and Standing Stone Creek watersheds (Figure 3-1). Each of these fluvial systems contributes to the Juniata River watershed, a major tributary of the larger Susquehanna River, that drains to the Chesapeake Bay. Specifically, the study sites were spread along these wetland riparian zones to include interior, mature forest tracts within Rothrock State Forest, recently logged and immature forest stands in the Stone Valley Forest (Penn State's Experimental Forest), and nonforested and agricultural private property located to the southwest of these public lands. This configuration allowed the sites to include a variety of land cover types and represent the overall forest disturbance gradient found in this study region. Thus, most of the study sites were within close proximity (100 m) to these floodplain dominated corridors. This is of no great surprise, however, since often, wetland patches provide the only remaining undisturbed habitats in human modified areas and provide much of the habitat for native wildlife (Serfass and Brooks 1998). The study sites consisted of forested slopes, stream banks, agricultural fields and a diversity of other sites along these riparian ecosystem zones. Using areas surrounding riparian wetlands provided excellent opportunities to study these research questions by providing significant forest cover gradients.
Figure 3-1. Map of riparian study sites (n = 23) in the Ridge and Valley Province of central Pennsylvania. Green shading denotes forested land cover and yellow shading marks nonforest. Sites are classified into five groups based on interior conditions (percent interior forest) and are represented as colored dots transitioning from red to green as the amount of interior forest increases.

Methods

[1] Site Selection

The research sites used for this study were selected from locations already regularly examined for Riparia's other projects. These reference locations were originally established by random selection along riparian corridors and wetland zones. Specifically, these established 222 Riparia study locations were chosen from a listing of candidate sites that "were selected at
random from a regional pool of sites developed from U.S. Geological Survey (USGS) topographic maps, National Wetland Inventory maps, and Natural Resource Conservation soil surveys" based on a variety of factors including yearly accessibility, wetland classification, geographic distribution, and randomness (Brooks et al. 2013a p54). For more information on the selection of these sites, please consult Chapter 2 of Mid-Atlantic Freshwater Wetlands: Advances in Wetlands Science, Management, Policy, and Practice (Brooks et al. 2013a).

I selected from this grouping of sites by bounding watershed areas in central Pennsylvania as defined by the specifications of the appropriate USGS Hydrologic Units (HUCs). Specifically, I systematically selected sites to represent the variety of land cover characteristics throughout my study area to represent different forest cover percentages and levels of human modification. Sites were selected along a gradient of landscape disturbance and are located along two stream networks within my research area. Originally, 24 priority study sites were selected. However, due to last minute complications with private land permissions, several backup sites were substituted and access was granted for 23 sites. The precise locations and orientation of the camera traps at the selected sites varied so that the most likely places for detecting the target species were used for camera locations. Specifically, I aimed the cameras at existing game trails and areas with less vegetation to increase the likelihood of wildlife detection (Figure 3-2).

Figure 3-2. Example sites for forested (left) and nonforested (right) riparian zones.
I obtained land cover datasets that accurately quantify forest cover and other landscape metrics by using applicable remote sensing and land cover classification techniques. This quantification was necessary to ensure that a substantial forest cover gradient was examined. The two datasets collected for further landscape metric analysis were both regional sections of the National Land Cover Database commissioned by USGS (NLCD 2007). Both datasets from 2001 and 2006 have a 30-m resolution and were used to compare results across the past decade of human development. In addition, a 2007 orthoimagery dataset with a resolution of 0.3 m (1 ft) commissioned through the PAMAP Program was used to visually inspect the accuracy of the previously mentioned land cover datasets for each of the site locations (PAMAP 2006). This dataset was commissioned by the Bureau of Topographic and Geologic Survey under the Pennsylvania Department of Conservation and Natural Resources (DCNR). In addition, on the ground-truthing of each site during field data collection was also used to confirm the accuracy of these landscape datasets. All of these datasets were acquired via the Pennsylvania Spatial Data Access online resource (PASDA). Another dataset that was inspected and found redundant was the percent tree canopy layer from the National Land Cover Database commissioned by the USGS (NLCD 2007). This dataset did not provide any additional information to the other land cover datasets as it was derived from the same source material.

Specifically, these land cover datasets were analyzed using the software program Fragstats (McGarigal et al. 2012) that is designed to derive a variety of habitat metrics from categorical land cover maps. A few of the landscape metrics that were selected for this project are Percent Forest Cover, Mean Patch Size, Percent Interior Forest, and Edge Density. These indices provided different measures of the landscape characteristics of the study areas and a base to analyze how these characteristics affect wildlife populations. In addition to forest cover and land
cover datasets, there was also a need for datasets outlining protected areas, wetland inventories, fluvial networks, road networks, and digital elevation models. These were obtained to see which variables best explained the habitat preferences of the mesopredators. However, the primary datasets collected and used in this study were derived from the National Land Cover Database commissioned by USGS.

In addition to these landscape analyses, environmental metrics were also taken at each site while in the field. Both the Stream-Wetland-Riparian (SWR) and Mid-Atlantic Rapid Assessment Protocol (MARAP) indices were used to characterize each study site and quantify onsite habitat variables such as corridor width and the number of invasive species (Brooks et al. 2009, Brooks et al. 2013b). These indices provided excellent onsite metrics to analyze a variety of habitat characteristics that could be relevant to the predator species. These assessments were performed independently in the summer months for each of the 23 sites. For more information on these assessments consult Brooks and Wardrop (2013). Survey forms for each of these assessments are included in Appendix B for a more detailed look into the methods involved and the significance of the results. However, only the relevant metrics to mesopredators in each of the assessments were used for further analysis. For instance, riparian corridor width is likely to be much more important to terrestrial mammals than the channel substrate composition, which is more likely to be relevant to aquatic macroinvertebrates. The specific metrics from these assessments that proved to be relevant to the predator community are discussed at length in the results section of this manuscript.


For this project, I monitored the distribution, composition, and population of mesopredator species on the selected sites along this forest cover gradient by using a number of
different techniques. As previously mentioned, I define mesopredators for the purposes of this study as mesocarnivores: medium sized carnivorous and omnivorous mammals that have historical or current distributions in the Mid-Atlantic Region (see Table A-1 for species list). To spatially monitor these organisms, I used tactics that did not require direct contact with the animals. I used the systematic placement of 24 camera traps and scent lures to examine the community dynamics of mesopredators in the area. While a relatively new data collection approach, camera trapping provides a robust method to sample for rare species (such as those targeted in this study) and has been implemented in a growing number of studies, specifically with predators (Thompson 2004, O’Connell et al. 2010). As I previously mentioned, I relied on a systematic site selection method from Riparia’s randomly selected reference sites, within the boundaries of the reference watershed study area, to identify the locations for camera traps and lures.

The study sites were located within 100 m of a stream bank within the riparian zone. Two cameras were placed at each of 12 study sites, facing in different directions. The geographic locations for all of these camera placements were recorded in latitude and longitude using a Garmin Etrex (Garmin Ltd., Olathe, KS). For each camera placement, I setup the camera traps for two weeks with scent lures and bait to attract nearby wildlife to the site. Two weeks is a sufficient period of time to fully sample the predator population in the immediate study area and has been used as a time interval in similar studies (e.g., Smith 2012, Cove et al. 2012) Camera traps were revisited once per week to gather picture data, check batteries, and re-scent the lure for the second week. After two weeks of sampling, I repeated this procedure by placing the 24 cameras in my remaining, unsampled locations for another two weeks. After the second two weeks period, I retrieved the cameras and analyzed the data they collected. To summarize, approximately a month of data collection was conducted, sampling 23 total study sites with two cameras engaged at each site. However, data collection did not occur at every site simultaneously. This data
collection cycle was utilized in all four seasons, to account for seasonal variation in the wildlife community. The same 23 areas were sampled once per season, for a total of four seasonal samples per site location. Thus, in total, there was four months of data collection. While my data collection periods did not fall precisely within any one month, the general months when data was collected were April, July, October, and February. These seasonal sample periods were targeted at the apex of each season, to capture the most seasonal variation.

Figure 3-3. Example of deployed camera trap and scent lure at each site.

In regards to the data collection itself, the cameras were targeted at analyzing the presence and relative abundance of carnivore species. This collection strategy also makes it possible to analyze the predator community as a whole, instead of only individual species. When an animal was detected, the motion sensor cameras were set to record three rapid images of each specimen along with a date, time, and temperature stamp. The cameras used in this study were Covert (Lewisburg, KY, http://covertscoutingcameras.com) brand trail cameras that were motion triggered and featured an infrared flash. This style of cameras have a low level of influence on their subjects and often go completely unnoticed (O’Connell et al. 2010, Meredith 2008). These
cameras were chosen to preserve natural behavior in the photograph subjects. Each of these camera traps was anchored to a tree approximately 0.75 m off the ground using cable locks and bear cartridges. Every camera was aimed at an area that appeared to be most heavily used by animal traffic such as game trails and clearings. A scent lure was hung with fishing line directly in front of one of the cameras at the site. The lure was approximately 2 m from the cameras motion sensor and approximately 1 - 2 m above the ground.

The assortment of scents applied was aimed at attracting a wide array of carnivores: one for the mustelids, one for the canids, one for the felids, and one for wetland obligate species, such as mink and otter. These scents were applied to cotton balls inside the scent lures to better absorb and emit the scents. In addition, to attract those carnivores less receptive to scent lures, small amounts of bait were also left below the scent lures. While the bait varied across each season, it usually consisted of a portion of meat and some slices of fruit. Finally, each of the scent lures was fitted with hanging chicken feathers to provide a visual stimulus to attract species less interested in scents or bait, such as bobcats. This scenting and baiting technique appeared to attract a large variety of carnivore species and resulted in frequent camera triggers.

Photographed species were identified using the Peterson Field Guide for Mammals of North America and with the assistance of resident mammalogists in Riparia (Reid 2006). Every animal that triggered the cameras was recorded. The presence and relative abundance of these species at each of these different locations allowed for the calculation of mesopredator species richness and habitat occupancy at each of these sites (Thompson 2004, O’Connell et al. 2010, MacKenzie et al. 2002). In addition, the time table of the project allowed seasonal changes in relative abundance, occupancy, and species richness to be analyzed for each species (Thompson 2004, O’Connell et al. 2010, MacKenzie et al. 2003). However, this is not without significant limitations especially given the need to individually identify each recorded specimen to analyze the absolute abundance of each species (Thompson 2004, MacKenzie 2006). Using the time and
date stamps as well as the geographic locations, I was able to analyze the seasonal activity times and behavioral patterns of the mesopredators. To accomplish this, I had to first create an index of possible behaviors such as foraging, hunting, socializing, etc. (Table A-3). This index along with the record of activity times was then used when analyzing behavioral patterns.

In addition to the cameras and lures, an assistant and I also conducted field transects to search for trace evidence of these mesopredators such as tracks and fecal material. Transect walks for each site were performed in each season after the camera data collection was complete, totaling four transect rounds for each study site. In winter, track evidence could be uniformly distributed and was more visible, providing the best chance to observe predator footprints. In light of this, an extra transect was conducted at each site during this period, 24 - 36 hours after freshly fallen snow. Thus, in winter two transects were conducted for each site. All of the transects were systematically spaced, with walking lines approximately 10 m apart and surveying a total area of roughly 500 m$^2$ (0.05 ha) surrounding each camera location. In addition, the search for trace evidence was not constricted to those systematic transects. Anytime trace evidence was discovered while working at or traveling to the sites, it was catalogued or collected. Each observation of trace evidence was either photographed or collected for further examination to ensure correct mesopredator identification. Species trace evidence was identified through the assistance of resident mammalogists in Riparia and by using the track plates described by Reid (2006). Unlike the data collected by the camera traps, this trace evidence could not be used in any abundance calculations, rather these data were used only to confirm the presence of particular carnivore species and compare to the occupancy results captured by the camera traps at each of the study sites. Only when these occupancy results did not roughly correspond were these trace evidence results analyzed further.
[4] Data Preparation and Analysis

After a year of data collection and preliminarily examination, I moved forward with analysis. In the course of these analyses, I relied on a variety of software packages including ArcGIS, R-project, Fragstats, and Presence (ESRI 2013, R Core Team 2013, McGarigal et al. 2012, and Mackenzie 2006). I used the GPS coordinates collected in the field to map the locations of each site. Next, all of the aforementioned landscape datasets were included for analysis for these site locations. Once these datasets and locations were mapped together in ArcMap using the Albers Equal Area projection to minimize areal distortion and compatibility issues between UTM and state plane projections, I created site buffers with radii of 500 m and 1,000 m on which to extract environmental variables. Using these enclosing buffers, a map for each landscape variable at each study location was created for the 1,000 m and 500 m scale. These maps were then used for all of the subsequent landscape metric analysis (Figure 3-4).
Figure 3-4. Example site buffers (1 km radius) with land cover. The black center dots are the actual site locations and the land cover maps represent the landscape up to 1km from the study site. The site buffer on the left illustrates a forested site with minimal disturbance and only two land cover types: forest and developed. The site buffer on the right illustrates a disturbed site dominated by agriculture and pastured lands. The site is also adjacent to development.

[a] Landscape and Environmental Analysis

The main bulk of this landscape analysis was centered on the two land cover datasets provided by USGS. However, before any landscape analysis could be performed, these land cover maps needed to be reclassified. Specifically, these maps were classified in ways that were relevant to the species in question. Each dataset was classified in two ways. For the first classification scheme, the datasets were classified to merge all of the developed portions of the landscape into one developed class. In addition, all of these forested classes were merged to create a single forest landscape class. No other changes needed to be made as most of the land cover types were not represented in the buffered circles around each of my study sites and were thus ignored. Therefore, the first classification scheme that these 23 sites could be composed was divided into five different land cover classes: forested, developed, cultivated, pasture, and open water. These classes were used as they seemed relevant to the species at hand. However, to simplify the analysis further, a binary classification was also created from this previous classification scheme, with the simple classes of forest and nonforest. Open water, while included in nonforest, made up such a small proportion of the landscape that it was unlikely to skew landscape analysis in any meaningful way.

Using Fragstats, both of these classifications (for both 500 m and 1 km circles) were analyzed using a variety of landscape metrics aimed at targeting both the composition and configuration of the landscape. Metrics examining both landscape and land cover class characteristics were used. Some of the metrics examined were as follows: Contagion, Edge Density, Percent Forest, Percent Nonforest, Percent Interior Forest, and the Percentage of Like
Adjacencies. Since several of these metrics are related and some are simply the inverse of each other, only the most relevant were used for each species (e.g., nonforest for foxes and interior forest for bobcats). For more information about the calculations behind each of these metrics, consult the Fragstats help manual (McGarigal 2014).

In addition to the landscape analyses, site level analyses were performed using the environmental data collected while in the field. This data consisted mostly of the SWR and MARAP assessments already mentioned, but also included densitometer canopy cover measurements. However, only a few site-level metrics were thoroughly analyzed in conjunction with the dynamics of the carnivore community and most of these revealed the quality of the riparian corridor itself (e.g., width and vegetated structure). After calculating these metrics, the respective values were associated with each study site for subsequent analysis with the predator occupancy and abundance data to address my original hypotheses.

After evaluating these metrics, it was apparent that the 23 sites selected for this study spanned a gradient from completely forested sites with wide riparian corridors to highly disturbed sites lacking riparian corridors with natural woody vegetation. Some study sites were influenced by a variety of human disturbances including frequent road use and noise, hunting pressure, agricultural cultivation, domestic animals, and mechanical vegetation disturbance. However, other sites, were influenced minimally by humans during the study period (e.g., an occasional hiker) and a few had no observed human presence for the course of the project. Table A-4 in Appendix A provides a summarized breakdown of environmental characteristics for each site.

Landscape metrics provided some of the most powerful and easily quantifiable results, while site-level assessments provided information that could not be detected from a landscape level analysis. Measures such as Percent Forest Cover and the number of edges per hectare (Edge Density) proved particularly useful. To evaluate the observed landscape gradient that was captured by these selected sites, sites were grouped qualitatively by taking into account the level
of human disturbance observed at each site using the previously described environmental metrics. However, choosing any one metric would have led to disparate and misleading results and so multiple metrics were used and analyzed to create this more descriptive classification of each site. For instance, a few highly disturbed sites had relatively wide riparian corridors, but most of the other factors indicated a more heavily disturbed classification. Based on these qualitative categories, roughly an even number of each classification was confirmed: eight sites were categorized as having a low level of overall disturbance, eight with a medium level of disturbance, and seven with a high level of disturbance. Nevertheless, even though multiple metrics were used to create these levels, these classifications lined up perfectly with a gradual decline of Percent Interior Forest at each site location. In short, these sites could be ranked using Percent Interior Forest as well as these qualitative categories and achieve similar results. Thus, these sites were evenly distributed across the landscape gradient along riparian corridors in an attempt to include as many environmental conditions as possible. This shows that the sites met the original goal expressed during the site selection process: to represent the entirety of this rural landscape along these riparian corridors. Due to the subjective nature of these qualitative categories, however, only the individual environmental metrics were used in further analysis. In addition, the binary classification scheme of forested and nonforested proved to have the most significant results as related to carnivore occupancy and abundance. Thus, though the majority of metrics were calculated for both schemes, the binary classification dominates these results and proved the most useful. The results for every variable, unless otherwise indicated, were calculated using the binary classification scheme of forest and nonforest.

In regards to these individual landscape metrics a variety were used in this analysis and addressed either the composition or configuration of the landscape, with a few addressing both. However, only a few were reliably correlated and associated with carnivore occupancy and abundance. If the variable had a correlation coefficient above 0.6 and was significantly associated
with carnivore occupancy or abundance repeatedly, it was deemed an important variable. The correlation coefficients for these most important variables are included in Table 3-2, located in the results section. These most important environmental metrics are identified in this table and the variables used in further analysis are marked with an asterisk. A more specific account on how these variables were chosen will be explained in the next section. However, before I report more results, it is important to briefly explain the calculation of each variable (also see Table 3-1). These explanation are derived from the Fragstats help documentation, compiled by Kevin McGarigal, that can be downloaded here:

http://www.umass.edu/landeco/research/fragstats/documents/fragstats.help.4.2.pdf

Edge Density, Percentage of Like Adjacencies, Percent Adjacent Forest, and Percent Pasture had the four highest correlation coefficients (all above 0.7). Edge Density is simply the average number of edges (areas with different adjacent land cover types) per hectare on the landscape. It is expressed with the following equation: \( \text{Edge Density} = \frac{E}{A} \times 10,000 \) where \( E \) is the total length (m) of edge on a landscape and \( A \) is the total area (m) of the landscape. The Percentage of Like Adjacencies is simply the sum of like land cover class adjacencies over the total number of possible adjacencies presented in a percent. This is calculated using the double count method to preserve pixel order and is represented by the following formula: \( \text{Percent Like Adjacencies} = \frac{\sum L_{\text{Adj}}}{T_{\text{Adj}}} \times 100 \) where \( L_{\text{Adj}} \) is the corresponding number of adjacencies in the same class and \( T_{\text{Adj}} \) is the total number of possible adjacencies. Percent Adjacent Forest is the same as the above measure but calculated for only one land cover class, forest. Percent Pasture is easy to calculate as the number of pixels classified as pasture over the number of total pixels formatted as a percentage of the total landscape.

Seven other metrics had correlation coefficients between 0.6 and 0.7 and were sometimes significantly associated with carnivore occupancy and abundance. Area Weighted Fractal Dimension is a metric aimed at explain the complexity of landscape shapes and edges. For more
information about this metric, consult Fragstats help documentation or the relevant literature. Contagion is essentially the proportional abundance of each land cover class as compared to proportion of adjacencies to other land cover classes. In short, when one class dominates the landscape, Contagion is relatively high. Contagion is fundamentally the inverse of Edge Density. For more information on Contagion, please consult relevant Fragstats help documentation.

Percent Interior Area is the sum of core areas in each patch of a landscape for a particular land cover class divided by the total landscape area and then formatted into a percentage. In short, Percent Interior Area equals the percentage of the landscape comprised of the core area of a particular patch type. Percent Forest, Nonforest, and Developed are calculated the same way as Percent Pasture. These composition metrics are simply the area of the class in question over the total landscape area, formatted into a percentage. Riparian Zone Width Score is the only metric listed here that did not have a landscape component. Instead, this score was derived from the field-based portion of the SWR Assessment, specifically the EPA Rapid Bioassessment (Figure B-1). This score ranged from 1 to 20 based on the site habitat characteristics. In short, the higher the score, the wider and more vegetated the corridor. Descriptions explaining how each site was scored can be found in Figure B-1. Many other metrics were not included here or used in subsequent analysis because they were either not significantly associated or highly correlated with these measures of the carnivore community.

In addition, several of the above metrics (and a few others) were combined using a previous formula developed by Riparia for cataloging the overall Stream – Wetland – Riparian Condition (SWR). This formula is as follows: \[ SWR \text{ Landscape Index} = \text{Average [Percent Forest + (Land Diversity Index + Impervious Surface Area)/2 + (Average Forest Patch Size + Percent Interior Forest)/2]} \]. However, this overall SWR Landscape Index did not prove to be highly relevant for these carnivore species, while some of the individual metrics included within it did. These and other relevant metrics are included in the following results section.
Table 3-1. Definitions of various landscape metrics briefly summarized from a more thorough description in the body text.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edge Density</td>
<td># of edges between classes per hectare</td>
</tr>
<tr>
<td>Percent Like Adjacencies</td>
<td>ratio of adjacent cells in the same class to total</td>
</tr>
<tr>
<td>Percent Adjacent Forest</td>
<td>ratio of adjacent forested cells to all adjacencies</td>
</tr>
<tr>
<td>Percent Forest/Pasture/Etc.</td>
<td># of cells of a class over the total number of cells</td>
</tr>
<tr>
<td>Area Weighted Fractal Dimension</td>
<td>weights edge complexity between land classes</td>
</tr>
<tr>
<td>Contagion</td>
<td>abundance of a class by its other adjacencies</td>
</tr>
<tr>
<td>Percent Interior Area</td>
<td>ratio of interior cells in a class to total cells</td>
</tr>
<tr>
<td>Riparian Zone Width Score</td>
<td>SWR qualitative ranking of riparian width health</td>
</tr>
</tbody>
</table>

[b] Community Level Richness and Abundance Analysis

To analyze the relative abundance and species occurrence values of the mesopredator community in conjunction with these aforementioned environmental covariates, three main strategies or levels of analysis were used. First, both overall site species richness and relative abundance were analyzed using simple correlation and regression techniques in an attempt to separate the most important environmental covariates that should be used in the further levels of analysis. Specifically, all of the measured environmental variables were analyzed with both the abundance and species richness values. Using the correlation coefficients and linear regression significance and \( R^2 \) values, nine of the most significant and best fitting environmental covariates were identified and used in subsequent analysis. In addition, these nine covariates were selected to eliminate redundancy (e.g., did not include both Edge Density and Contagion) and with all the respective species’ habitat preferences in mind (e.g., nonforest for generalists and interior forest for specialists). In addition, the species richness and relative abundance results were also
analyzed across each of the four seasons to determine if any seasonal variations were evident. These differences were not statically calculated, rather described and visualized.

[c] Individual Species Occupancy Analysis

Due to the inherent invalidity of these abundance data both on the species level and overall, a second method of analysis was needed. For this approach, each species was analyzed individually and then the carnivores were classified by taxonomic and ecological groups (e.g., canids or specialists) in conjunction with the previously identified environmental metrics. In this second stage of analysis, the presence and absence of each species and the relative abundance of each species was analyzed across study sites, along these multiple variables. It is important to note, that for most of the species, the relevant abundance measures were discounted and the observed presence and absence of each species at each side was deemed preferential. This is due to the difficulties surrounding the individual identification of the carnivores that trigger the cameras. This preference served to eliminate any bias in these data that could lead to disproportionately high carnivore abundance estimates. This strategy is due in large part to the recommendations of my colleagues in Riparia and an examination of recent camera trap literature (e.g., Gompper et al. 2006, Cove et al. 2012). The only exception to this preference was in the examination of species that were virtually present in every site (e.g., raccoons and opossum). For these species, I was forced to continue using relative abundance as any presence/absence analysis would show no difference along these environmental covariates. Thus, for these two species a simple regression approach was used. However, it is important to remember that repeat occurrences of these species, if they occurred within 10 minutes of each other, were removed. Thus, a reasonable attempt was made to correct the relative abundance values of these species. Nevertheless, for the rest of the species, a different approach was needed to analyze the binary, presence/absence data.
To analyze these species individually (and by taxonomic and ecological groups) using only this presence and absence at each site, a logistic regression approach was needed. This logistic transformation of a simple linear regression leads to models that fit binary response data, such as the presence and absence of these species, using a maximum likelihood approach. This is a common method of analysis for camera trap and trace evidence data, when individuals cannot be identified (Thompson 2004 and O’Connell et al. 2010). In addition, these analyses were performed for each site in each season of data collection as well as across all four seasons. However, due to the nature of this analysis the bulk of the following discussion will be limited to whether these species occupy the habitat patches in question and will not include discussions of density or absolute abundance. The results of both of these levels of analyses are reported below in the species richness and relative abundance section of the results.

As already mentioned, the results from camera traps are often used to simply test whether a species is likely to be present or absent at a particular site, a measure of the likelihood that it occupies a particular location. These likelihoods can then be linked to habitat or environmental covariates that are then tested to see if they can accurately predict the habitat occupancy of the species in question. And while this is usually only performed at an individual species level, some data aggregation is possible (i.e., grouping species by like ecological characteristics). Nevertheless, this method of analysis provides powerful and reliable results, similar to the regression analysis of species richness discussed previously. Both of these measures remove a great deal of doubt by not dealing with possibly inaccurate measures of abundance, once again since individual species were not identified. Instead, the only substantial source of doubt that remains is in determining whether a species is actually absent from a particular site if it does not trigger one of the camera traps (i.e., the probability of detection). Due to this difficulty, two levels of occupancy analysis were needed. First, the simple logistic regression approach previously described ignores the probability of detection (actually assumes it is 100%). However, once this
first approach yielded significant results, a more robust occupancy modeling strategy was used. But before this is described, it is important to note that the data collected from these camera traps mostly represents the movements of these species and is, therefore, biased toward movement behaviors and characteristics. Thus, these occupancy results should not be misconstrued to represent all aspects of a species’ daily activities (e.g., denning, resting, etc.). More precisely, these data show habitat occupancy or use only for the mobile and more active moments of these carnivores’ lives. For a full listing of the site occupancy for each species and each study site, see Table A-5 in Appendix A. In addition, this occupancy analysis can only provide statistically powerful and significant results if subjects occupy a moderate number of sites. If species occupy too many sites or too few, significant relationships with measured environmental variables are unlikely to be found. The species that fit this moderate occupancy parameter were bobcats, coyotes, and both species of foxes.

Thus far in the analysis, it was evident which species and groups seem to be most affected by landscape differences along the riparian corridors in my study area and which covariates were most important to explaining these habitat preferences. However, the previous levels of analysis make a large and invalid assumption, that if a species did not trigger a camera at the site, it was not present at that site. This violates an important assumption about absence that is discussed at length in ecological literature (MacKenzie 2006). In short, it is extremely difficult to confirm the absence of a species and there is always some level of doubt that a species is actually not present at a site even when it was not observed. To quantify this doubt (or probability), I needed a more refined modeling strategy. Thus, I used a more advanced occupancy modeling technique, whenever possible.

For this more robust occupancy modeling approach, I used the program Presence (MacKenzie 2006). This program is designed to take these probabilities of absence (actually probability of detection) into account and has been used in a variety of studies with camera traps
(e.g., Meredith 2008, Cove et al. 2012, Long et al. 2011). Basically, this modeling technique can report on everything that a simple logistic regression can (probability of presence, power of covariates, etc.), but it takes the probability of false absence into account (MacKenzie et al. 2002, Mackenzie et al. 2003, Mackenzie and Royle 2005). It is also important to note that to estimate detection probability, there must be more than one survey of each site. In other words, the results from multiple surveys, or in this case, periods when the cameras were deployed, are used to calculate how often a species is detected or not detected at each site. This ratio is used to create a probability of detection, that is then applied to all of the occurrence results.

For this analysis, I defined a survey or sample period as the period of time cameras were deployed after scents were applied to a site. These were approximately one week periods. Due to my study design and the repeated scenting of each site, there were two of these designated surveys periods each season for a total of eight surveys at each site for the entirety of this project. Technically, one could have defined these surveys in numerous ways such as the number of individual days that cameras were deployed at a site. However, since the scents were used to draw in these species and since individual days cannot be treated equally in terms of the likelihood of carnivore occurrence (i.e., scents likely decreased in potency as each week progressed), it made sense to treat the deployment of scents as independent surveys of these study locations. In addition, using individual days would have resulted in artificially low probabilities of detection due to the life history characteristics of these species (e.g., home range size and activity patterns), thereby skewing the results of this analysis.

To determine if the probability of detection influenced the relationships witnessed in previous levels of analysis, I need a three step approach to create robust occupancy models. First, I ran occupancy models on the influence of the site environmental covariates previously described on the probability of occurrence of various carnivore species. Then, I created occupancy models to see if these covariates influence the probability of a species triggering the
camera. This is a measure of the probability of detection (and an indirect measure of the likelihood of absence) for each species in question. Finally, I ran occupancy models taking both of these probabilities into account in a combined, even more robust analysis. This technique was based on Mackenzie’s multiple publications on this subject and the advisement material included with the Presence program (MacKenzie et al. 2002, Mackenzie et al. 2003, MacKenzie and Royle 2005, MacKenzie 2006). However, because of the nature of these models, their assumptions, and general requirements, this Presence program was only used to analyze carnivore species where relationships and trends were perceived to exist based on the previous levels of analysis. Thus, if a species was too rare (e.g., Martes pennanti) or at every site (Procyon lotor), it was not analyzed using this method. This is because these analyses would result in findings that are virtually no different from those already seen in the simple logistic regression models previously described.

[d] Species Activity and Behavior Analysis

Once a complete analysis of these carnivores in conjunction with environmental covariates was performed and the impacts of each of these covariates documented (on every species and among multiple groups), I also analyzed the activity patterns and behavioral differences among the carnivore species. While this was not the original goal of this study, the data was available due to the time stamps and behavioral observations collected from the camera trap photographs. For this analysis, I constructed graphics representing the circadian rhythms and behavioral patterns of the most common carnivores. These circadian rhythm graphs are simply 24-hour clocks with the cumulative frequency of carnivore occurrence in each hour zone being visualized. In short, the times with the highest frequency of a carnivore species will be readily visible in the graphic. This provides the viewer with a useful estimation of the average activity pattern of a particular species. For the behavioral analysis, I lumped the previously delineated behavior classes into three classes for analysis: foraging, vigilant, and traveling. This type of classification can be used to describe behavioral patterns and observed differences among the
target species, which will be described in the following section (O’Connell et al. 2010). However, since this portion of analysis was not considered when this study was designed, I did not perform any statistical analysis on this data. Instead, I simply visualized it and described any observed trends or patterns.

Overall, the methods of this study seek to measure the habitat occupancy and landscape preferences of the entire group of mesopredators, smaller functional subsets, and individual species. However, a supplemental analysis of behavior, relative abundance, and activity patterns is also important to understanding how these species use their landscape and interact with one another.

For clarity, the following results section is divided among the previously outlined levels of analysis, with the exception of the landscape analysis section. The following section begins with the simple regression results of measures such as species richness and culminates in several occupancy models for a few carnivore species. Overall trends for the community and each species are also enumerated.

**Results**

[1] *Community Species Richness and Relative Abundance*

When examining the community as a whole, several interesting patterns were immediately apparent. First, the composition of the mesopredator community was dominated by just two species, raccoon and opossum. Together these two species accounted for almost 90 percent of the observed carnivore occurrences, even after these results had been corrected for repeat camera triggers by these species. The next most abundant species were bobcat and black bear, respectively. The most abundant species after those two were red foxes, domestic cats, and
coyotes. The other species: skunks, fisher, mink, domestic dog, and gray fox, each accounted for less than 1 percent of the observed carnivore detections (Figure 3-5).

![Relative Abundance (Percent)]

Figure 3-5. The approximate relative abundance of species in the predator community. Every percentage value has been rounded to the nearest whole number while each colored portion represents the actual relative abundance of each given species. The abundance of the other, less abundant species is outlined in the subplot to the right of the primary pie graph. Opossum and raccoon dominate this graphic as a result of their higher relative abundance.

Another trend that is apparent after a brief analysis was that species richness was highly correlated with several environmental variables (Table 3-2). Similar correlations were found in each of the four seasons, but are discussed cumulatively here. The most correlated variables were Edge Density, Percent Adjacent Forest, and Percent Like Adjacencies, all measures of the level of fragmentation in a landscape. However, metrics examining landscape composition also exhibited
strong correlations, such as Percent Forest, Percent Nonforest and Percent Pasture. Finally, metrics that take both composition and fragmentation (or configuration) into account are also important (e.g., Percent Interior Forest). To visualize these results, I included scatter plots in Figure 3-6. As is visible in both Table 3-2 and Figure 3-6, some of these metrics exhibited negative correlations and others exhibited positive relationships. The possible reasons behind these trends will be examined later. These strongly correlated site metrics were then analyzed further so that the importance of these relationships could be assessed. Particularly the metrics marked with asterisks were analyzed further. These metrics were selected for their strong relationships and because they represent several different measures. However, some measures were calculated so similarly that it only made sense to use one of them. For instance, both Percent Like Adjacencies and Contagion are calculated using the same techniques that are used to calculate Edge Density (in fact Percent Like Adjacencies is essentially the inverse of Edge Density). Therefore, only Edge Density was used for further analysis. The only exception to this was in the case of forest and nonforest (which are also the inverse of each other) due to a desire for a positive relationship to be found for each species (i.e., some species will prefer forest and others will prefer nonforest). However, these variables were not used simultaneously in the models.

Table 3-2. Species richness correlation coefficients for each environmental metric. Metrics designated for use in subsequent analyses are marked with an asterisk adjacent to the correlation coefficients.

<table>
<thead>
<tr>
<th>Site Metric</th>
<th>Correlation Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area Weighted Fractal Dimension</td>
<td>0.61*</td>
</tr>
<tr>
<td>Contagion</td>
<td>-0.66</td>
</tr>
<tr>
<td>Edge Density</td>
<td>0.71*</td>
</tr>
<tr>
<td>Percent Adjacent Forest</td>
<td>-0.72*</td>
</tr>
<tr>
<td>Metric</td>
<td>Value</td>
</tr>
<tr>
<td>--------------------------------------------</td>
<td>--------</td>
</tr>
<tr>
<td>Percent Interior Area</td>
<td>-0.67*</td>
</tr>
<tr>
<td>Percent Developed</td>
<td>0.65*</td>
</tr>
<tr>
<td>Percent Forest</td>
<td>-0.64*</td>
</tr>
<tr>
<td>Percent Like Adjacencies</td>
<td>-0.71</td>
</tr>
<tr>
<td>Percent Nonforest</td>
<td>0.64*</td>
</tr>
<tr>
<td>Percent Pasture</td>
<td>0.70*</td>
</tr>
<tr>
<td>Riparian Zone Width Score</td>
<td>-0.65*</td>
</tr>
<tr>
<td>SWR Landscape Index (combined)</td>
<td>-0.47</td>
</tr>
</tbody>
</table>
Carnivore Richness By Edge Density

Carnivore Richness By Interior Forest

Percent Interior Forest

Carnivore Species Richness

Edge Density (edges per hectare)
Figure 3-6. Example scatterplots of several important metrics by species richness with best fitting regression lines. Carnivore species richness increases as Edge Density (or fragmentation) increases but decreases as both Percent Interior Forest and Riparian Zone Width increase.

First, after examining these coefficients and the scatter plots, there was little evidence to support a nonlinear relationship. The next steps for analysis involved creating linear models. Taking the outlined correlations further, simple linear regression analysis showed significant associations with many of these environmental variables. Particularly, four environmental metrics stood out as both explaining a good portion of the variance in the data and exhibiting highly significant relationships (those previously listed with the four highest correlation coefficients). However, a full breakdown of the significance and $R^2$ values for each of the previously mentioned metrics designated for further analysis is included in Table 3-1. Every variable was
analyzed individually and then the most powerful predictors were combined in an attempt to create the best model for explaining species richness through landscape and site-level variables.

Table 3-3. Species richness linear regression results for the most important environmental variables. Significance levels are marked by asterisks and are denoted below the table.

<table>
<thead>
<tr>
<th>Site Metric</th>
<th>Coefficient</th>
<th>p-value</th>
<th>R² value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area Weighted Fractal**</td>
<td>14.412</td>
<td>0.00211</td>
<td>0.3391</td>
</tr>
<tr>
<td>Edge Density***</td>
<td>0.04682</td>
<td>0.00013</td>
<td>0.4855</td>
</tr>
<tr>
<td>Percent Adjacent Forest***</td>
<td>-0.07603</td>
<td>0.00011</td>
<td>0.4193</td>
</tr>
<tr>
<td>Percent Developed***</td>
<td>0.033254</td>
<td>0.00078</td>
<td>0.3951</td>
</tr>
<tr>
<td>Percent Forest***</td>
<td>-0.03328</td>
<td>0.00093</td>
<td>0.3858</td>
</tr>
<tr>
<td>Percent Interior Forest***</td>
<td>-0.03310</td>
<td>0.00052</td>
<td>0.4164</td>
</tr>
<tr>
<td>Percent Nonforest***</td>
<td>0.03328</td>
<td>0.00093</td>
<td>0.3858</td>
</tr>
<tr>
<td>Percent Pasture***</td>
<td>0.05367</td>
<td>0.00019</td>
<td>0.4660</td>
</tr>
<tr>
<td>Riparian Zone Width Score***</td>
<td>-0.20116</td>
<td>0.00083</td>
<td>0.3920</td>
</tr>
</tbody>
</table>

Significance Symbols: '***' 0.001  '**' 0.01  '*' 0.05 '.,' 0.1

Thus, every metric exhibited a significant association with species richness. However, as displayed in Table 3-3, Edge Density, Percent Interior Forest, Percent Adjacent Forest, and Percent Pasture were the best predictors of species richness based on both their high level of significance (p-values less than 0.0005) and the large proportion of variance explained (R² values over 0.4). Closely following these four variables was Riparian Corridor Width and Percent Developed. Since Riparian Corridor Width were a source of ground truthing to these other metrics (site level metric), and both variables were also highly significant, they were included for
further analysis as well. In short, these six variables best explained species richness along riparian corridors and so they were combined in a cumulative linear model. However, when these six variables were combined into an additive model, the result was not ideal. While, the adjusted R^2 increased to 0.5335, none of the variables remained significant predictors of species richness on their own, though Percent Adjacent Forest and Edge Density remained close to being significant. Therefore, this model needed to be condensed.

To further analyze this possible trend, I used an all-subsets regression to analyze each different combination of these variables. This analysis is used to determine which model fits best by explaining most of the data. It is important to note that the best model is usually the model that can explain the most variance and is simultaneously the simplest. The results of this more advanced analysis were not surprising. The best and simplest model was one that only included the two variables that remained the closest to significant in the original additive model: Percent Adjacent Forest and Edge Density. This has an R^2 of 0.61 indicating that it explained approximately 60 percent of the variation in species richness in these sites along riparian corridors. In addition, both metrics remained significant predictors and will be used throughout the remaining analyses with other predictors periodically supplemented as proves appropriate, though all of the previous outlined metrics were analyzed at each subsequent stage, even though the results may not be reported. Only the most appropriate and significant variables for each species or measure will be mentioned in the remainder of this manuscript. Table 3-4 below has a full breakdown of this model. Once again, the significance levels are symbolized.

<table>
<thead>
<tr>
<th>Site Metric</th>
<th>Coefficients</th>
<th>p-values</th>
<th>DF</th>
<th>R^2 value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent Adjacent Forest**</td>
<td>0.01697</td>
<td>0.00929</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 3-4. The best fitting, linear predictive model for species richness. Significance levels are marked with asterisks and denoted below the table.
So far, only species richness has been thoroughly discussed. While relative abundance is not as statistically sound as species richness, it does illustrate some interesting patterns. For instance, it can be used to show differences in site level abundance both to compare carnivore species and see differences across different seasons (Figure 3-7). It is important to remember, however, that the relative abundance measures derived from camera traps are crude attempts to account for the abundance of these species, since individuals are fully capable of returning to the site and be counted again throughout the sampling season. In reality, these measures are more representative of the frequency that these species visit these corridor sites rather than the density or abundance of these carnivores across the landscape itself. In addition, the observed seasonal patterns for most of these species are tenuous at best, due to their rarity. Thus, seasonal patterns will not be discussed thoroughly in this thesis. Nevertheless, using frequency as opposed to occupancy does provide an interesting look into the relative abundance of each species, the carnivore community composition, and the seasonality of these carnivores, at these study locations.
Figure 3-7. A graph denoting site abundance in the predator community by season. This figure shows the variation in carnivore occurrences based on season. For instance, the black bear did not occur in winter but occurred more often in fall.

In addition, to simply visualizing these abundance data overall, it is also possible to analyze these data by species and in response to particular habitat and landscape variables, as was previously completed with the carnivore species richness as each site. Similarly, both correlations and linear regressions were used to examine these relationships. However, the statistical power and validity of these analyses must also be thoroughly examined.

Overall, carnivore abundance increased with increasing fragmentation and decreasing forest cover however, this trend was not significant. After further investigation, the lack of
significance could be tied to one particular species, the opossum. This is displayed in Figure 3-8 and 3-9 that illustrate the overall carnivore abundance trends followed by that of the opossum. As one can see, the same two outliers and general lack of trend for the bulk of the scatterplot is present in both graphs. This striking similarity is due to the overwhelming abundance of the opossums that washed out all other trends in these data. On that note, it is important to remember how abundant the raccoons were as well and with the opossums removed, they too would dominate these abundance results. Because of the dominance of these two species, they were both removed from this analysis and analyzed individually. With the raccoons and opossums removed, an abundance trend did become significant and fit the data much better. This new relationship can be seen in Figure 3-9, that shows how the site abundance of the remaining carnivores is related to fragmentation. In short, as Edge Density increases, so too does mesopredator abundance (p-value = 0.001, $R^2 = 0.37$). However, because the abundance counts of these other carnivores are so low, this graph and result is not fundamentally different from the species richness results. In fact, the graphs appear identical except that the species richness results fit these data better including raccoons and opossums.
Figure 3-8. A scatterplot with a regression line showing predator abundance by edge density. A general upward trend is evident but so are two possible outliers in the top right corner of the scatterplot. These points may be disproportionately influencing the trend line.
Figure 3-9. A scatterplot with a regression line showing opossum site abundance by edge density. Note that two possible outliers are also present, indicating a similarity between the two scatterplots and trends. Removing opossums from the original scatterplot may remove these possible outliers.
Figure 3-10. A scatterplot with a regression line showing carnivore site abundance by edge density, this time without opossums or raccoons. Removing these two species also removed the possible outliers that were disproportionately influencing the regression fit. The removal of these species lead to a better fitting, linear abundance model.

Nevertheless, though these overall abundance results were significant and interesting, these results did not offer a better prediction of individual species habitat preferences (or overall species richness) than just recording the presence and absence of each carnivore at each site. On an individual basis, the only species that showed different habitat preferences using the abundance data as opposed to the presence and absence data was the raccoon. Overall, raccoons were more abundant in fragmented sites than they were in forested sites. Specifically, the results showed that raccoons were significantly more abundant in sites with a higher level of
fragmentation (p-value = 0.005, $R^2 = 0.27$) and narrower riparian corridors (p-value = 0.04, $R^2 = 0.14$). This relationship was present in every season except winter when raccoons were extremely rare. These abundance trends are important due to the presence of raccoons at every site. Therefore, without abundance data, nothing could have been said about raccoons’ habitat preferences along these riparian corridors. With that said, while these trends are significant, they explain very little of the variability in raccoon abundance along these riparian corridors as they seem to be abundant at most sites.

However, since this was the only instance of this difference and since determining species habitat preferences and occupancy is the key goal of this project, the results for the other species will not be mentioned here. After all, the occupancy analysis in the next section is more robust and designed to answer specific questions about habitat preferences.

[2] Habitat Occupancy of Individual Species

Dealing first with the logistic regression analysis, only three canid species demonstrated significant habitat occupancy preferences in terms of the landscape variables I measured: red foxes, gray foxes, and coyotes (Table 3-4). Surprisingly, even though bobcats appeared at roughly the same number of sites as these species (a moderate number), logistic regression analysis showed no pattern based on the habitat and environmental variables that I measured (Table 3-5). This is demonstrated by the pr-values, the significance indicator for logistic regression measuring the probability that site occupancy is not influenced by the explanatory variable. In short, the environmental variables measured in this study did not appear to impact bobcat site occupancy. However, the logistic regression analysis I performed on each of these canid species showed that they all preferred more fragmented sites than did other mesocarnivore species and, as seen in the table below, they preferred areas with higher edge densities. The two fox species showed the
strongest and most consistent habitat occupancy trends. In fact, they were so similar that it was even possible to combine the two fox species and still show strong patterns in habitat preference. In addition, the patterns in fox presence and absence seemed to hold true using many different habitat metrics. For instance, as illustrated in the logistic regression graph, foxes are much more likely to be present at a site when the proportion of nonforested area is high (Figure 3-11). This was actually the best variable for predicting the presence of foxes with a probability value of 0.005 and an AIC of 19.58, 3.54 lower (and thus better fitting) than the combined logistic regression model including three related variables. This trend held true when examining Percent Pasture though this variable proved slightly less significant and redundant. Based on these values, Percent Nonforest makes for a better predictive occupancy model and shows a more significant pattern. This is visible in the spatial pattern of the fox occurrences as well (Figure 3-12).

Table 3-5. The habitat occupancy of canids and felids by Edge Density. Both canid species have significant pr-values indicating a significant relationship with Edge Density as well as lower AIC values than did bobcats indicating the established model better fit the occurrence data.

<table>
<thead>
<tr>
<th>Site Metric</th>
<th>Coefficient</th>
<th>pr-values</th>
<th>DF</th>
<th>AIC value</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Foxes</td>
<td>0.07075</td>
<td>0.0208*</td>
<td>21</td>
<td>26.564</td>
</tr>
<tr>
<td>Bobcats</td>
<td>0.00308</td>
<td>0.872</td>
<td>21</td>
<td>35.815</td>
</tr>
<tr>
<td>Coyotes (With Trace)</td>
<td>0.04906</td>
<td>0.0450*</td>
<td>21</td>
<td>30.410</td>
</tr>
</tbody>
</table>

Significance Symbols: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1
Figure 3-11. Percent Nonforest and the occupancy of both fox species. A value of 1 indicates that foxes were present at a site and a value of 0 indicates that fox presence was not recorded. Based on these occurrence values, a best fitting maximum likelihood model was created. The model fit line shows the nonlinear increase in occupancy probability as related to Percent Nonforest. This model illustrates that fox occupancy was significantly associated with Percent Nonforest and that as the amount of nonforest increases, so too did the probability of fox occupancy.
Figure 3-12. Locations of red and gray fox occurrences in the study landscape. Green represents forested and yellow, nonforested landscapes. The red dots are proportionally related to the number of fox appearances in a study site and the black dots represent sites where foxes were not recorded during the study. The location of these occurrences fall almost entirely in agricultural or edge-forest locations, indicating that foxes exhibited a habitat preference toward these portions of the landscape.

However, the landscape preference of coyotes was much more tenuous. First, the coyotes only appeared at a few sites in terms of triggering the camera traps. Using only this portion of the data, no significant trend could be seen in habitat preferences. However, I then added the coyote trace evidence dataset to the camera trap dataset, after which this trend became visible and significant. Importantly, coyotes seemed to be present in many sites even when they did not trigger the camera trap, according to this trace evidence data. Coyotes are the only species that showed such a discrepancy. This discrepancy is displayed in Figures 3-13 and 3-14. As an
example, on two occasions recorded in the field, I witnessed coyote tracks turn to move in front of the camera, only to stop and travel in the opposite direction before triggering the camera. These instances combined with the discrepancy I witnessed imply that the coyotes might have been avoiding the camera traps. Thus, this weak significant trend was only present when trace evidence was included. This trend is best demonstrated in Figure 3-15 where it is more evident that coyotes were usually present in the moderately and highly disturbed sites, while likely absent in the interior forest riparian sites (pr-value = 0.045; AIC = 30.41, ΔAIC = 4.404).

Figure 3-13. Coyote occurrence locations detected by camera traps across study landscape. Green represents forested and yellow, nonforested landscapes. The orange dots are proportionally related to the number of coyote appearances in a study site and the black dots represent sites where coyotes were not recorded during the study. With these few disparate occurrences identifying habitat preferences was difficult.
Carnivore Occupancy - Coyote

Figure 3-14. Coyote appearances as evidenced by tracks at sites where cameras failed to record presence. Green represents forested and yellow, nonforested landscapes. Once again, the orange dots are proportionally related to the number of coyote appearances in a study site and the black dots represent sites where coyotes were not recorded during the study. The purple circles represent study locations where the cameras did not record coyote presence but where coyote tracks were found. After adding in this trace evidence, the preference of coyotes to occupy forest edges and nonforested areas became more apparent.
Figure 3-15. Coyote presence and perceived absence by Edge Density. After adding in the trace evidence locations, the logistic regression analysis also showed a significant trend in terms of coyote site occupancy. Once again, a value of 1 indicates that coyotes were present at a site (and were observed either via camera traps or tracks) and a value of 0 indicates that coyote presence was not recorded. Based on these occurrence values, a best fitting maximum likelihood model was created. The model fit line shows the nonlinear increase in occupancy probability as related to Edge Density. This model illustrates that coyote occupancy was significantly associated with Edge Density and that as fragmentation increases, so too does the probability of fox occupancy.

These logistic regression results were further analyzed using Presence to account the probability of detection at each of these sites. This additional analysis was only conducted for coyotes, foxes, and bobcats as the rest of the species were either too abundant or too rare for this more robust occupancy modeling approach.
Not surprisingly, similar to the logistic regression results, bobcat occupancy did not seem to be influenced by any of the habitat variables tested. In fact, the AIC values for the base model that did not include the habitat variables was almost the same or lower than the models that included habitat variables, indicating that a model that failed to include habitat parameters was in line with the best fitting occupancy model for bobcats. However, the most telling result of this analysis was the difference between the naïve occupancy estimate, or the occupancy value assuming the probability of bobcat detection was 100% (i.e., no false absences), and the actual occupancy estimate, or the occupancy value using the calculated probability of detection derived by the model (i.e., includes false absences). The model calculates the actual occupancy estimate by referencing the number of observed occurrences versus the number of observed absences at locations where bobcats were observed to be present. Essentially, the model calculates the probability of recording a false absence. Thus, this actual occupancy estimate was roughly 8% indicating that 92% of the time bobcats were observed as absent even at sites where bobcats were known to be present. The naïve occupancy estimate calculated that the probability of bobcats occupying a site was roughly 48% meaning that bobcats would probably be present at one out of every two sites. When taking into account the calculated probability of detection, however, the actual occupancy estimate came to 100%, indicating that the differences in occupancy among sites were likely due to the probability of detection and not distinct habitat preferences. This actual occupancy estimate held for almost every habitat covariate tested. The only exception to these trends occurred when Riparian Zone Width was included in the model, as can be seen in the slightly lower AIC value for the model, indicating a slightly better fit. However, the ΔAIC, or difference between this and the next lowest AIC value, was minimal at 0.15. Nevertheless, when including this variable, the actual occupancy estimate fell in some sites based on the value of this variable. In sites classified as having narrow riparian corridors, the probability of occupancy fell to approximately 80%. Nevertheless, this robust occupancy modeling approach further
emphasizes the results of the simple logistic regression analysis, that bobcat occupancy seems largely unrelated to the environmental variables measured in this study.

Coyotes exhibited some of the same difficulties with this approach as did the less numerous species, especially before the addition of trace evidence to the occurrence results. According to the naïve occupancy estimate, coyotes were estimated to occupy 56% of the study sites. However, when taking into account probability of detection (8% for both camera and trace surveys combined), coyotes were expected to occupy every site. However, once environmental variables were included, this pattern changed. According to this analysis, Percent Nonforest was the most important for this species, with an AIC value 1.76 lower than a model including no environmental variables, resulting in individual occupancy estimates for some of the more forested sites to fall as low as 59%. More importantly, the derived parameters of this model at some of the sites were as low as 38%, when taking into account both the probability of detection and occupancy. This indicates that at some of the less disturbed sites, coyotes are only 38% likely to occupy a site, or occur there only around one instance in three. Nevertheless, coyotes were still more likely to occupy most sites using any one of these environmental covariates. In short, this robust analysis serves to weaken the observed relationship seen when running simple logistic regression analysis. This is due to the exceptionally low probability of detection.

The two fox species once again demonstrated the most powerful trends. The naïve occupancy estimate was approximately 39% and the actual estimated occupancy before covariates were added was only 58%. Percent Nonforest was the most important variable for these canids as well with an AIC value 5.6 lower than the base model with no environmental covariates. The probability of detection for this species held around 13% for this species as well. However, despite this low probability of detection, the derived parameter for this model was also low for some sites, as low as 27% in some instances. This indicates that at some of these forested sites, the probability of a fox occupying the site when taking into account both the probability of
detection and the probability of occurrence is only around a one in four chance. This shows that environmental covariates likely influence fox occupancy, even when taking into account false absence or the probability of detection. Similar to the coyotes, while the relationships observed in the simple logistic regression models were weakened once again, they did not disappear completely, indicating they remain important relationships.

However, despite these seemingly interesting results and the additional evidence that some of these carnivore species are associated with certain environmental covariates, it is possible that some of these models did not converge and that these data did not fully support this analysis method. In addition, while the probability of detection did not seem to vary in any of these datasets as a response to the environmental covariates used, they did have an impact. In other words, some of the differences in occupancy witnessed in these species may actually be due to the impact that some environmental covariates have on the probability of detection and not the probability of occurrence. This is just a possible variable that should be mentioned. It is more likely, however, that this modeling approach introduced a more substantial level of doubt than was justified. After all, these robust occupancy models were not designed for use with continuous camera traps, but rather discrete site surveys. This original design explains the models overemphasis on correcting for false absences and thus, the artificially low probability of detection it calculates. Indeed, missing an individual when one is surveying a site one foot once or twice is not the same as missing that same individual after having sampled for two weeks at a site with a remotely triggered camera trap. In most instances, the camera trap is far more likely to record an occurrence due to its prolonged presence and covert placement. This is especially the case with these rare mammals due to the secretive nature and larger home ranges of these elusive species.

While other models have been developed in an attempt to better fit this approach to camera trap studies, the data collected in this study did not lend itself well to these other
approaches. For instance, a multi-season model might have lessened the impact of the nondetections on sites known to have certain carnivores occupying the site. This is simply because this approach would have divided up these detections (or lack thereof) and not have calculated them cumulatively at each site across all four seasons. However, as mentioned previously in this manuscript, these species were simply too rare to divide the data by season. Doing so would have resulted in just two or three occurrences per season across 23 sites for a number of species. This would have led to little or no statistically significant results. In short, even with the logistical changes made to these data and attempts to make them better fit this approach, there were still not enough occurrences to support a truly robust occupancy model, especially if data were further divided by season or some other temporal variable. Nevertheless, these results do indicate habitat preferences in these three canid species and that these preferences are reflected in the landscape and site level metrics measured for this project.

Other than these three canids, no carnivore showed consistent occupancy differences or habitat preferences along these riparian corridors. This was surprising in some cases, for instance, neither bobcat nor mink, generally considered habitat specialists, demonstrated significant occupancy patterns based on these landscape variables. Both species appeared to use multiple site types across the landscape gradient (Figures 3-16 and 3-17). The other species were either too rare (e.g., skunks or fisher) or showed a similar lack of habitat preference (e.g., raccoons or opossum) when analyzing these data by these landscape metrics. In fact, since raccoons and opossums were present at virtually every site, no meaningful occupancy analysis could be performed for these species (see Figures 3-18 and 3-19).
Figure 3-16. Locations of bobcat occurrences in the study landscape. Green represents forested and yellow, nonforested landscapes. The blue dots are proportionally related to the number of bobcat appearances in a study site and the black dots represent sites where bobcats were not recorded during the study. These occurrence locations were spread throughout the landscape and do not indicate a strong habitat preference.
Figure 3-17. Locations of mink occurrences in the study landscape. Green represents forested and yellow, nonforested landscapes. The blue dots are proportionally related to the number of mink appearances in a study site and the black dots represent sites where mink were not recorded during the study. These occurrence were rare and were spread throughout the landscape and so, do not indicate a strong habitat preference.
Figure 3-18. Locations of raccoon occurrences in the study landscape. Green represents forested and yellow, nonforested landscapes. The blue dots are proportionally related to the number of raccoon appearances in a study site. Raccoons occurred at every site and thereby did not exhibit habitat occupancy preferences. However, the relative abundance of raccoons at these study sites showed that raccoons were more common in edge and disturbed sites.
Figure 3-19. Locations of opossum occurrences in the study landscape. Green represents forested and yellow, nonforested landscapes. The blue dots are proportionally related to the number of opossum appearances in a study site and the black dots represent sites where opossum were not recorded during the study (two sites). Opossum occurred at almost every site (21 of 23) and thereby did not exhibit habitat occupancy preferences.

However, it was possible to analyze these abundant species’ (raccoon and opossum) habitat preferences by season. Namely, I analyzed the occupancy data for both raccoons and opossums in each season to determine if there habitat preferences changed depending on the time of year. While both raccoon and opossum did appear at fewer sites in winter, the decline did not display significant trends. Rather this declined occurred in all habitat types and seemed to be associated solely with a uniform decline in winter abundance. Therefore, no seasonal differences were found based on the measured habitat variables and no qualitative patterns were evident from this analysis. So, the results of this analysis are not included in this manuscript.
With these quantitative results in mind, a more qualitative assessment of the behaviors and activity patterns was performed to add context to these occupancy, richness, and abundance measures.

[3] Species Activity and Behavior

As previously mentioned, the observed activity and behavior of these carnivore species was not analyzed using statistical models. Instead, patterns were visually examined to see if patterns or differences could be seen broadly in these data. Overall, some interesting trends were visible, both in the circadian activity patterns of the most abundance species and in some behavioral differences between various carnivores.

To begin, the circadian rhythm graphics for most of the species were simply too sparse (due to a low amount of recorded occurrences) to show strong trends. However, for the two most abundant species, raccoons and opossum, particular patterns in activity can be seen in the graphs. For instance, the observed raccoons were almost exclusively nocturnal with their activity peaking around midnight (Figure 3-20a). This nocturnal pattern did not seem to fluctuate across seasons. However, the opossums exhibited a somewhat different trend, that was primarily nocturnal, but with an earlier activity peak, about 7:00 pm, or dusk (Figure 3-20b). However, unlike crepuscular species, the opossums were active into the night and were generally not active at dawn. Unlike the raccoons, this trend did fluctuate during the winter season when opossums shifted their activity period into the daytime hours, possibly due to the severe cold after nightfall. Opossums do have bare skin and are more susceptible to frostbite and cold weather (Elbroch and Rinehart 2011).
Figure 3-20a. Overall circadian activity graph of raccoon occurrences. The graphic represents the frequency of raccoon occurrences within one hour intervals of a 24-hour clock. Raccoons occurred most often between the 20:00 and 0:00 indicating that the species is strictly nocturnal and attains its peak activity level from dusk until midnight.
Figure 3-20b. Overall circadian activity graph of opossum occurrences. The graphic represents the frequency of opossum occurrences within one hour intervals of a 24-hour clock. Opossum occurred most often between the 18:00 and 0:00 indicating that the species is strictly nocturnal and attains its peak activity level from dusk until midnight. However, in more than a few instances, opossums occurred during the daylight hours. All of these instance occurred during the winter sampling season indicating that opossum may shift their active period into the warmer daytime period during the cold winter months.

In terms of the behavioral patterns observed in this study by these camera traps, some interesting differences among the species were observed. While baiting the traps did bias the behaviors of these species toward more foraging responses, this analysis does not seek to examine the natural activities and behavior of these carnivores. Rather, these comparative analyses of the main types of behaviors exhibited demonstrates how these species react to human influences or stimuli such as baited stations, abnormal scents, and other disturbances in their local environment. Behavioral data were analyzed to see if some species proved to be more vigilant or were more interested in the attraction of scents than some of their predator counterparts.
The vast majority of the behaviors exhibited could be categorized into three behavior groups: movement, foraging, and vigilance. Using these groupings, several patterns became visible. First, raccoons and opossums seemed to spend most of the time in front of the camera exhibiting foraging types of behavior such as smelling the ground and eating (Figure 3-21). In contrast, both bobcats and coyotes spent the majority of their time either moving through the landscape or exhibiting vigilant types of behavior such as being watchful or looking at the camera. Interestingly, many other species (e.g., foxes, skunks) seemed to split their time fairly equally between these multiple behaviors while in front of the cameras. It is important to mention again that the cameras did not shoot continuously, but instead provided a sample of the behaviors by shooting three photographs every 30 seconds when triggered. Thus, while these patterns are interesting and imply some behavioral differences among these species, these results are not as powerful as they would have been if the cameras had been recording video continuously or taking pictures more frequently. Nevertheless, these results are useful in conjunction with the habitat occupancy analysis to present a more complete picture of the community dynamics of these species and how they use riparian corridors.
Figure 3-21. Behaviors exhibited in each recorded occurrence for each carnivore species. Every behavior exhibited by these species was categorized into one of three behavior groups: those exhibiting movement, vigilance, or forage. This graph shows that some carnivore species exhibited different behavioral trends than others in the study locations. For instance, opossum and raccoons spent most of their time foraging or moving while bobcats and red foxes spent a considerable time exhibiting vigilant types of behaviors.

Clear and concise conclusions can be drawn both for several individual species and for the community overall. But in drawing these conclusions, it is important to interpret these results with reference to the expected patterns based on the life history characteristics of these species and the literature on the mesopredator release hypothesis. In some cases, the results are consistent with expectations. However, several of these observed results are surprising and demonstrate that some of these predators may behave differently than previously believed or react to landscape differences unexpectedly, at least in central Pennsylvania.
Chapter 4

Implications, Discussion, and Conclusions

This project analyzed the composition and habits of the mesopredator community in central Pennsylvania across seasons and the landscape in a manner that did not disrupt the natural behavior of the target species and allowed for an intimate look into their use of their environment.

The predator community as a whole behaved in a way that was somewhat surprising when considering my original hypotheses. My original expectations were consistent with the intermediate disturbance hypothesis, namely that the community would have the highest species richness and abundance on the edge or intermediately disturbed sites (Connell 1979). However, this hypothesis appears to have been incorrect for this system. Instead, both species richness and abundance peaked at the most highly disturbed sites. While this may be puzzling at first, it actually is not upon further investigation. Many studies have shown that various mesopredators peak in abundance in areas of intermediate disturbance (e.g. Prange and Ghert 2004, Ordeñana et al. 2010, Crooks 2002), however, these studies usually include urban or suburban areas as their highest level of disturbance, with developed rural landscapes as their intermediately disturbed areas. In addition, and as Yahner (1988) emphasized, it is difficult to determine what constitutes an edge (or an edge effect) for a species, especially in a field setting. It is likely that at least some of these species did not experience any practical edge effects (or conflicting ones), as they may have been able to use different aspects of each land cover type and thus, the whole landscape (Yahner 1988). Therefore, with those preferences and previous studies in mind, it is not as surprising that the species richness of the carnivore community in my study area peaked in these developed rural locations, where a greater diversity of habitats were likely to be present together,
because severely disturbed habitats were likely not represented and the disturbance present in my
study area may not deter these mesopredators as much as I first expected. However, assessing the
impact of edge effects and disturbance on these species is difficult and requires further study.

When looking at the results for the community as a whole (or the individual species
results together), another important conclusion needs to be drawn. Almost every species was able
to use the human portion of these landscapes in some way, even species previously considered
habitat specialists. But without qualification, this conclusion would be misleading and not
supported by the collected data. This is because my study only applies to these carnivores’ use of
riparian corridors and the not the entire landscape. This project does not provide any evidence to
support assertions about how these species behave away from riparian zones. Therefore, this
conclusion can be revised to say that the majority of these carnivore species are able to utilize
riparian corridors in human dominated landscapes, even some species previously described as
habitat specialists.

Riparian corridors seem to be extremely important to some of these species and are
perhaps the reason they use these portions of the landscape at all. Many carnivores would likely
be able to exist in these rural human landscapes even if the last remnants of natural vegetation did
not exist. But for those species generally considered habitat specialists (e.g., mink, bobcat, and
even black bear) these riparian zones likely provide suitable pathways for movement into these
cultivated agricultural lands. Therefore, in terms of my original hypotheses, my expectations were
incorrect once again and that generalists and specialists did not react as I predicted along these
riparian corridors.

As far as identifying habitat specialists, however, the results were surprising. First, I am
referring to habitat specialists as those species that require specific landscape characteristics, such
as wide riparian corridors. Thus, by this definition, bobcats seemed to be more of habitat
generalists than the fox species that were limited to the human disturbed portions of the corridors.
Even coyotes seemed to avoid the interior forest corridors the majority of the time. However, these conclusions should be qualified. It is possible that both the fox species and coyotes used interior forested areas, but had no need to travel along the riparian zones and were able to spread out in the forests and move more quickly (Elbroch and Rinehart 2011). Therefore, these riparian corridors could have served as a funnel, focusing their movement, when they moved into disturbed portions of this rural landscape (Lindermayer and Fischer 2006). However, this was probably not a common practice for these species (with the possible exception of the gray fox) based on their life history characteristics. For instance, red foxes generally do prefer open areas and are, therefore, unlikely to use interior forest zones (Elbroch and Rinehart 2011).

Nevertheless, these results demonstrate that canid species tend to become less common in wide, forested riparian corridors. In this regard, my original hypothesis appears to have been correct in that species in the group Canidae in my study area do seem to be associated with disturbed habitats. If these canids target prey species that tend to occupy human-dominated areas (e.g., eastern cottontails or gray squirrels), then they would be expected to select these areas of higher food availability. In addition, other anthropogenic sources of food such as refuse and domestic animals may further incentivize the use of human landscapes (Roemer et al. 2009). However, to fully understand these observed patterns a study that includes prey species dynamics and food availability is probably necessary. In short, these canid species usually considered habitat generalists did demonstrate specific habitat preferences in a way that other specialists did not.

One of the most important findings of this study was the disproportionate dominance of just two species in this landscape. Raccoons and opossum accounted for the majority of detections in this study. They were also the most abundant after repeat triggers had been removed when comparing relative abundance patterns. While this is not wholly unexpected since one would think these smaller species would be more common than their larger cousins, their abundance seemed disproportionate when compared to other similar studies (e.g., Kelly and
Holub 2008). In addition, in statistics published by the Pennsylvania Game Commission, opossum and raccoon accounted for 12% and 35% of all fur bearer harvests, respectively, and 15% and 44% of all fur bearing carnivore harvests, in the wildlife management unit encompassing my study area (Lovallo and Hardisky 2012). Thus, these two species accounted for just under 60% of harvested carnivores, well below the almost 90% of carnivore occurrences at my study locations. Nevertheless, because actual abundance was not calculated with identified individuals, this conclusion is uncertain. Nevertheless, two species accounting for almost 90 percent of carnivore occurrences seems extreme along these riparian zones, even for a disturbed system.

In the entire study period, no species (other than raccoons and opossums) occurred more than 16 times (out of 132 days across four seasons at 23 sites), the total occurrence value for bobcats, indicating most of these carnivores were extremely rare. However, for the less rare species: raccoons, opossums, bobcats, coyotes, and foxes it is not unreasonable to draw conclusions. Canids showed statistically significant preferences that, for the most part, held when considering the probability of detection. Bobcats showed a surprisingly lack of preference and could have been at any site. Raccoons and opossums were at virtually every site.

In terms of my other hypotheses, the data collected really did not provide enough evidence to support reaching conclusions. There did not appear to be any evidence that one species excluded any others in terms of overall habitat occupancy. In fact, at one site the presence of a raccoon, bobcat, red fox, and coyote was all documented within a 24-hour period. In addition, the two species most likely to exclude one another, coyotes and foxes, did not seem to exhibit any noticeable interactions (such as coyotes supplanting foxes) in terms of site occupancy. Thus, while these species no doubt do interact, the predation and competition pressures they exhibit on each other may be too rare to fully initiate new behavior or distribution patterns. However, the rarity of these species once again comes into play, to truly deal with the interactions
these species have more study is needed, including more camera traps and other data collection techniques such as radio telemetry.

In terms of seasonal and temporal predictions, conclusions can only legitimately be drawn for the most abundant species, such as raccoons and opossums. For instance, the observation that opossums shift their activity patterns in winter to become more diurnal is quite interesting and consistent with the current understanding of the species in the life history literature (Elbroch and Rinehart 2011). Also, it was not surprising to find that raccoons and opossums were detected less during the winter season. As far as seasonal differences go, the vast majority of these carnivores were simply too rare to make even qualitative conclusions that could be reasonably separated from random chance. However, once again, opossums and raccoons did demonstrate differences in a way dissimilar to my expectations for generalist predator species. In short, their habitat preferences did not significantly change from season to season. Like most of the generalist mesopredators in this study, they seemed to use the majority of sites along the riparian corridor gradient.

As for my final study objective, it was possible to distinguish which landscape and site level characteristics were most important in predicting carnivore occurrence along these riparian corridors. Overall, landscape metrics that examined the configuration of the landscape seemed to be the most important for predicting species richness differences. Specifically, Edge Density (the number of edges per hectare) and Forest Adjacency (percent of forest patches adjacent to one another at each site) seemed to be important. Together, these accounted for more than 60 percent of the variation in species richness and were highly significant. While both of these were also important for individual species, some other metrics were also important when investigating individuals.

For the foxes, metrics measuring landscape composition, Percent Nonforest and Percent Pasture, were the most predictive metrics in terms of habitat occupancy. In addition, corridor
width also seemed to be fairly important both to predicting species richness and in showing trends among the various species. In fact, when many of the other metrics showed no trend at all, corridor width at least demonstrated that a trend might have been present if more data was collected (i.e., in the cases of mink, bobcats, and coyotes). In short, a few metrics did stand out in predictive power from the many others measured at these sites. However, there was no single variable to predict the occurrences of every species or the species richness and abundance of community as a whole. Indeed, there are likely many other non-landscape or site level variables that were not measured in this project that might explain the occurrence and habitat preferences of these species.

In terms of methods, this study does allow for important conclusions to be made regarding camera trapping as a methodology for studying rare species. Camera trapping provides a noninvasive way to study rare and elusive wildlife. Using this technique one can study their behavior, habitat preferences, and even abundance with certain study designs. However, this method does have significant limitations. Camera trapping will never replace the capture-mark-recapture approach as the most statistically viable and powerful abundance and density estimation method (O’Connell et al. 2010). However, if combined with the capture-mark-recapture method cameras can serve perfectly for the recapture portion of that approach. In other words, live recapture would not be necessary if the markings used were visible to the camera traps.

In addition, using camera traps to estimate density or catalogue habitat preferences are mutually exclusive goals. When estimating density, it’s best to avoid baiting the traps but to distribute them evenly across a known habitat area. However, when analyzing occupancy or habitat preferences, the cameras need to be more dispersed across a landscape of different habitat characteristics and baiting the traps is permissible. Therefore, this study employed the second approach and because of this, the strongest results and conclusions are drawn about habitat preference and site occupancy. Putting too much emphasis on the relative abundance results in
this study would be a mistake. However, relative abundance and frequency estimates can be analyzed in conjunction with habitat occupancy as a way of describing how occupied a site was among the different species in question. But, this is not to be confused with a population or density estimate.

As far as analyzing these species on the landscape and community level, this approach does have merit. This broader scale approach allows for researchers to examine the larger ecological system where these species exist. Targeting wildlife in guilds or groups also increases one’s ability to make broad conclusions about species communities. In fact, the breadth of this approach may be the only reason this study documented the occurrence of so many carnivores. A more targeted approach may have resulted in far fewer occurrences due to the mobility of these species and simply the random chance of incidence. However, the level of detailed results and conclusions for each species is diminished in this approach. Also, interactions between species are probably less definitive at this scale. Thus, for a more detailed approach into the behavior of individual species or the interactions between species, a more targeted approach is necessary such as a radio telemetry study.

There are some changes that could be made to improve this study approach. First, using multiple scents at the camera sites may have spooked the more skittish of these predators such as the coyotes. This is particularly true of species that may be subject to persecution by humans using poison bait stations and similar tactics. In addition, baiting the cameras in conjunction with the scents was probably not necessary. In fact, this modification may have actually influenced some of the more bold and oblivious mesopredators (raccoons and opossums), to simply linger at the sites and repeatedly trigger the camera, leading to an analysis problem that must be corrected later. Once again, the artificial presence of bait may also have deterred the more skittish of predators.
Another improvement that could have been made to this study design would be to aim the two cameras at each site at one another, in other words, at the same scent lure/bait station. This approach combined with a device to measure the size of the camera subject (such as a meter stick) would allow for a certain level of individual identification due to ability to photograph both sides of a carnivore in the search for unique markings or characteristics and measure the approximate the size of the subject. This technique could have allowed for an estimate of the absolute abundance of each species to be calculated at each study location. This recommendation is made mostly because aiming the camera in two different locations was not usually necessary and the vast majority of carnivores did trigger both cameras at a site in any particular instance. This new layout would strengthen the abundance results and would allow researchers to analyze the community composition in a more quantitative and statically powerful way.

Finally, adding more cameras and more sites, could increase the chances of capturing a carnivore on camera and would increase the statistical power of the results. More sites would allow more habitat types to be represented and more of the landscape to be sampled. In addition, keeping the cameras at the sites longer could have increased the likelihood of detection as well though it has been argued that two weeks is an optimal detection period (e.g., Smith 2012). However, leaving cameras at the same location too long, especially when baiting, may alter the behavior of the study subjects and create bait stations that the same individuals would repeatedly visit in search for food. This would violate the desire of researchers to not interfere with the natural patterns of the subjects and should be avoided.

Nevertheless, despite these limitation and suggestions for improvements, the results obtained from this study were informative. This study contributes toward understanding the mesopredator community in central Pennsylvania. This research project provided an accurate portrayal of how most mesopredators use riparian corridors along rural landscape gradients. The habitat preferences of these carnivores can be used in future studies that seek to analyze the
specific patterns and preferences each species demonstrates. Most importantly, this study emphasizes the importance of riparian corridors, even to highly mobile species such as carnivores. Thus, when policy makers seek to conserve or eliminate these types of species the importance of the riparian corridors should not be discounted.

This project contributes to the scientific understanding of the mesopredator community in that many of these species do use human landscapes in a way that their apex cousins did not. Thus, in rural settings similar to central Pennsylvania, these mesopredators are likely to compose a significant portion of the wildlife community and that portion is likely expanding. While more study is needed to fully understand how mesopredators use the entire landscape, how abundant they actually are and how they interact, it is obvious that they do live alongside humans. We need to understand what impacts these species have on ecological communities before the consideration of policies such as the selective elimination of certain groups. After all, these mesopredators perform important ecological services. The question is, will they remain out of balance with their ecosystems when their apex cousins are removed or attain some level of dynamic equilibrium? This question needs far more study before a suitable answer can be articulated. In an increasingly developed world, these mesopredators may be the only carnivores that can survive and thrive alongside humanity. That in itself makes them worthy of respect.
Appendix A

Study Tables

Table A-1. Mesocarnivore study species list.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
<th>Family</th>
<th>Order</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domestic Dog</td>
<td><em>Canis lupus familiaris</em></td>
<td>Canidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Coyote</td>
<td><em>Canis latrans</em></td>
<td>Canidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Gray Fox</td>
<td><em>Urocyon cinereoargenteus</em></td>
<td>Canidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Red Fox</td>
<td><em>Vulpes vulpes</em></td>
<td>Canidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Domestic Cat</td>
<td><em>Felis catus</em></td>
<td>Felidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Bobcat</td>
<td><em>Felis rufus</em></td>
<td>Felidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Black Bear*</td>
<td><em>Ursus americanus</em></td>
<td>Ursidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Raccoon</td>
<td><em>Procyon lotor</em></td>
<td>Procyonidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Striped Skunk</td>
<td><em>Mephitis mephitis</em></td>
<td>Mephitidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Least Weasel</td>
<td><em>Mustela nivalis</em></td>
<td>Mustelidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Long-tail Weasel</td>
<td><em>Mustela frenata</em></td>
<td>Mustelidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Mink</td>
<td><em>Neovison vison</em></td>
<td>Mustelidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Ermine</td>
<td><em>Mustela erminea</em></td>
<td>Mustelidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Fisher</td>
<td><em>Martes pennanti</em></td>
<td>Mustelidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>River Otter</td>
<td><em>Lutra canadensis</em></td>
<td>Mustelidae</td>
<td>Carnivora</td>
</tr>
<tr>
<td>Opossum**</td>
<td><em>Didelphis virginiana</em></td>
<td>Didelphidae</td>
<td>Dipdelphimorphia</td>
</tr>
</tbody>
</table>
* Categorized as an Apex Predator, *Ursus americanus* is the only remaining top predator in the region; *Canis lupus*, *Felis concolor*, and *Gulo gulo* are all believed to have been extirpated (Prugh et al. 2009, Merritt 1987).

** While not classified in the order Carnivora, *Didelphis virginiana* is regarded as mammalian mesopredator and is included in this study because it shares dietary and behavioral characteristics with the other mesocarnivores (Merritt 1987).

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Home Range Est.</th>
<th>Habitat Use**</th>
<th>Wetland Use***</th>
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<td>Beta</td>
<td>Upland</td>
</tr>
<tr>
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<td>75 - 650 ha</td>
<td>Gamma</td>
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*These data were collected from a variety of sources and serve as a gross simplification of the behavior and habitat requirements of each species (Merritt 1987, Kirkland and Serfass 1989, Croonquist and Brooks 1990, Brooks and Croonquist 1991). In addition, some
extrapolation of some habitat preferences and home ranges was required due to a shortage of data. This extrapolation was based on the requirements of similar species.

** The habitat use designation for the above species describes the habitat specificity required for a species to thrive. This habitat specificity can be divided into a spectrum of three groups: alpha (or specialist) species, gamma (or landscape dependent) species, and beta (or generalist, edge) species (Croonquist and Brooks 1990). This distinction is important as one would expect generalist species to fair better in more disturbed habitat and specialists to do worse (Croonquist and Brooks 1990, Croonquist and Brooks 1991).

*** Wetland use can be defined as the dependency of the species on wetlands. For the purpose of this study, the dependency of a species can be divided into three groups: obligate species that occur it wetlands 99% of the time, facultative species that rely on wetland zones to some degree, and upland species that generally do not require or use wetland areas (Kirkland and Serfass 1989, Croonquist and Brooks 1991).

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<th>Identifier</th>
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<th>Behavior</th>
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<td>INV</td>
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<td>EAT</td>
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This behavioral key will allow behavioral analysis to be run based on a variety of different environmental variables including, but not limited to: the season, the time of day, and a number of forest cover metrics. It will also account for the behavioral differences between each carnivore species recorded within the study area. This overall analysis could provide evidence demonstrating the different ways that mesocarnivores affect their ecosystem and other wildlife in that system, especially herpetofauna. Similar behavioral analyses have been conducted on a variety of organisms including: the gray snub-nosed monkey in China (Tan et al. 2013) and coyotes in California (Séguin et al. 2003).
Table A.4. Site environmental data summary with key disturbance metrics.

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<th>Disturbance Level</th>
<th>Land Ownership</th>
<th>Percent Forest</th>
<th>Percent Interior Forest</th>
<th>Edge Density (m/ha)</th>
<th>Corridor Width (m)</th>
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# Appendix B  
## Survey and Assessment Forms

Figure B-1. A portion of the Stream-Wetland-Riparian Assessment – EPA Rapid Bioassessment (Brooks et al. 2009).

### HABITAT ASSESSMENT FIELD DATA SHEET—HIGH GRADIENT STREAMS (FRONT)

<table>
<thead>
<tr>
<th>STREAM NAME</th>
<th>LOCATION</th>
<th>STATION</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>LAT</th>
<th>LONG</th>
<th>RIVER BASIN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>INVESTIGATORS</th>
<th>DATE</th>
<th>TIME</th>
<th>REASON FOR SURVEY</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Condition Category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suboptimal</td>
<td>Optimal</td>
</tr>
</tbody>
</table>

1. **Epithelial Substrate/Available Cover**
   - Score ranges: 10-9-8-7-6
   - Disease status: 5-4-3-2-1

2. **Embeddingness**
   - Score ranges: 10-9-8-7-6
   - Disease status: 5-4-3-2-1

3. **Velocity/Depth Regime**
   - Score ranges: 10-9-8-7-6
   - Disease status: 5-4-3-2-1

4. **Sediment Deposition**
   - Score ranges: 10-9-8-7-6
   - Disease status: 5-4-3-2-1

5. **Channel Flow Status**
   - Score ranges: 10-9-8-7-6
   - Disease status: 5-4-3-2-1

### Rapid Bioassessment Protocols For Use in Streams and Wadable Rivers: Periphyton, Benthic Macroinvertebrates, and Fish, Second Edition - Form 2

A-7
<table>
<thead>
<tr>
<th>Habitat Parameter</th>
<th>Optimal</th>
<th>Suboptimal</th>
<th>Marginal</th>
<th>Poor</th>
</tr>
</thead>
<tbody>
<tr>
<td>6. Channel Alteration</td>
<td>Normal or near-natural, stream with normal pattern.</td>
<td>Some channelization present, usually in areas of bridge struts/struts, evidence of past channelization, i.e., dredging. Minor erosion. Erosion causes velocity problems</td>
<td>Occasional channelization may be extensive; embankments or levees present on both banks, and 80% to 100% of stream reach channelized and disrupted.</td>
<td>Banks should be well-shaped, agree with stream slope, and channelized and disrupted. In-stream habitat greatly altered or removed entirely.</td>
</tr>
<tr>
<td>SCORE</td>
<td>20</td>
<td>19</td>
<td>18</td>
<td>17</td>
</tr>
</tbody>
</table>

| 7. Frequency of Riffles (or Bends) | Occurrence of riffles relatively frequent; ratio of distance between riffles divided by width of the stream is 15:1; riffles continuous, placement of boulders or other large, natural obstructions important. | Occurrence of riffles infrequent; distance between riffles divided by the width of the stream is between 15:1. | Occasional riffles or bends; bends continue provide some habitat; distance between riffles divided by the width of the stream is between 15:1. | Generally all flow water or shallow riffles; poor habitat; distance between riffles divided by the width of the stream is a ratio of >25. |
| SCORE | 20 | 19 | 18 | 17 | 16 | 15 | 14 | 13 | 12 | 11 | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 0 |

| 8. Bank Stability (score each bank) | Banks stable; evidence of erosion or bank failure absent or minimal; little potential for future problems. | Moderately stable; evidence of erosion and minimal potential for future problems. | Moderately unstable; 50-60% of bank in reach has areas of erosion. | Unstable; 60-100% of bank in reach has areas of erosion. |
| Note: Determine left or right side by facing downstream. | Moderate to severe bank instability; moderate to severe erosion. | Moderately unstable; 50-60% of bank in reach has areas of erosion. | Unstable; 60-100% of bank in reach has areas of erosion. |
| SCORE (LB) | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 0 |
| SCORE (RB) | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 0 |

| 9. Vegetative Protection (score each bank) | Greater than 50% of the streambank surfaces and immediate riparian zone covered by native vegetation, including trees, understory shrubs, or woody overstory; vegetation disruption through grazing or mowing minimal or not evident; almost all plants allow passive recruitment. | 50-50% of the streambank surfaces covered by native vegetation, but bare patches of soil or disturbed vegetation evident but not affecting fish growth potential or any great extent. | 30-50% of the streambank surfaces covered by vegetation, vegetation disruption evident but not affecting fish growth potential. | Less than 30% of the streambank surfaces covered by vegetation; vegetation disruption severe; fish growth potential greatly affected. |
| SCORE (LB) | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 0 |
| SCORE (RB) | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 0 |

| 10. Riparian Vegetative Zone Width (score each bank riparian zone) | Width of riparian zone > 10 meters; human activities have impacted zone only minimally. | Width of riparian zone 3-10 meters; human activities have impacted zone only minimally. | Width of riparian zone 0-3 meters; human activities have impacted zone significantly. | Width of riparian zone zone 0-3 meters; no riparian vegetation due to human activities. |
| SCORE (LB) | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 0 |
| SCORE (RB) | 10 | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 | 0 |

Total Score _____

A-8  Appendix A-1: Habitat Assessment and Physicochemical Characterization Field Data Sheets - Form 2
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