ABSTRACT

MILLER, ANNA BEHM. Impacts of Trail Building on Wildlife: A Before-After Control-Impact Experimental Study Using Camera Traps. (Under the direction of Dr. Yu-Fai Leung)

Protected areas are set aside from development to preserve natural ecosystems and frequently provide nature-based recreation opportunities. Recreational trails are linear infrastructures common to most protected areas, providing a path for humans to more easily travel through the natural landscape, but also concentrating their activity in certain areas. While nature-based recreation is important to maintain societies' connections with the natural world, it has also been documented to have negative effects on bird and mammal species, and may alter wildlife communities. However, most previous studies investigating interactions of humans and wildlife in rural recreation areas have been observational, lacking the ability to draw causal inference through a controlled experiment, and thus leaving much uncertainty as to the overall negative impacts of recreationists on wildlife.

The primary goal of this dissertation is to assess the impacts of trail building on the terrestrial vertebrate community. To achieve this goal, I first standardized a method to quantify both wildlife and human activity along hiking trails using motion-triggered cameras (camera traps) and field-based observation. This work showed that the optimal camera position should be: (1) directed towards locations where people move at approximately 8 kph or slower, (2) oriented at a shallow angle to the direction of movement, and (3) placed 1-2m from the trail edge. In my field trials, 82% of pedestrians and 75% of cyclists were detected by cameras set to these specifications.

To assess the impacts of new trail building on wildlife I used this optimal camera trap protocol in a before-after control-impact (BACI) experiment at a trail construction site in Stone Mountain State Park, North Carolina. I found that coyotes and white-tailed deer (*Canis*

latrans and *Odocoileus virginianus,* respectively) avoided the trail area during trail construction while raccoons (*Procyon lotor*) were attracted to the on-trail zone at this time. Surprisingly, overall species richness increased by 6.31 species in the on-trail zone during trail construction. After trail building was complete, eastern gray squirrels (*Sciurus carolinensis*) avoided the on-trail zone, and near-trail species richness decreased by two species, compared with pre-construction. Results were consistent with the human shield hypothesis, suggesting that smaller predators and prey species use human presence on and near the trail as a potential refuge from predation risk. Results also concurred with the mesopredator release hypothesis, with mesopredators such as gray fox (*Urocyon cinereoargenteus*) having increased detection rates in treatment zones during and after trail building while large predators such as coyotes and bobcats (*Lynx rufus*) avoided the human activity and thus had decreased detection rates in these zones and phases.

The relatively minor impacts of trail construction on wildlife suggest little conflict between trail-based recreation and wildlife at this study site. While statistically significant impacts were found, these were primarily restricted to the trail building phase near the area of construction activity and involved relatively minor changes in the activity of common species. Although not significant to wildlife conservation in this study area, these effects could have important implications in areas where endangered species are present, especially when trail building coincides with important life stages such as the breeding season. Managers can reduce the impacts of new trail building on endangered species by avoiding habitat and seasons most essential to these species. Future studies could use the method developed here to gather long-term, fine-scale spatiotemporal data on human-wildlife interactions.

Impacts of Trail Building on Wildlife: A Before-After Control-Impact Experimental Study Using Camera Traps

by
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DEDICATION

This dissertation is dedicated to family:

Fernando, my husband, who traveled with me across continents in pursuit of Douglas the Bear.

Rick, my father, who has a constant stream of ideas ready for my next dissertation project.

Susan, my mother, who finds it easiest to tell her friends I'm off chasing butterflies.

Sarah and Beth, my sisters, who still think it's an insult to tell me I dress like an ecologist.

I love you all and appreciate your encouragement along the way.

BIOGRAPHY

Anna is a North Carolina native. Her love for the outdoors blossomed at the age of six months upon her first taste of box turtle shell on a camping trip in the Appalachian Mountains. Her fascination with the natural world later led her to an ecology-focused study abroad program at the University of Lund, Sweden, which complemented her Bachelor of Science in biology at the University of North Carolina at Chapel Hill.

After completing her BS in Biology, Anna held several jobs before returning to graduate school. She first worked as a field technician at the Smithsonian Environmental Research Center, where she caught and tagged blue crabs in the Chesapeake Bay and learned about the ecological research process. She next decided to share her fascination with nature with elementary and middle school students as an outdoor science instructor in the San Bernardino Mountains of southern California.

Anna returned to graduate school in 2008. Through a collaborative international program, European Masters in Applied Ecology, Anna studied at four universities France, England and Germany, receiving Master of Science degrees from the University of Poitiers, France and University of Kiel, Germany. In this program she focused on fisheries management, interviewing artisanal fishermen along the coast of the Gulf of Lyon, France and performing statistical and spatial analysis to determine the impact of artificial reefs on these fisheries.

Upon completing her M.S., Anna returned to the US in 2010 and worked as a forest ecology lab technician at Duke University. During her doctoral degree she has taken opportunities to work as an intern and conduct research at Yosemite National Park, research and publish in community-based natural resource monitoring, write and assist with editing a Best Practices Guidelines for the International Union for the Conservation of Nature, volunteer for multiple projects in both social and ecological aspects of park management, and attend conferences on four continents. She plans to continue her career in human-environment interactions research, with a focus on the nature-based recreation context.

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Studying at North Carolina State University with such a supportive group of faculty, students, and staff, has been a wonderful experience for me. The opportunities to work collaboratively with students and faculty members in our college have helped me develop a broad understanding of both social and environmental aspects of parks, recreation, and tourism management. This environment has provided countless opportunities for academic, professional, and personal growth. I would like to give a special thanks to Dr. Dorothy Anderson, who asked important guiding questions and believed in this project from the beginning. I am also grateful for my research assistantship through the National Association of State Park Directors.

This project would not have been possible without the support of Wake County Parks and Recreation and North Carolina State Parks. Tim Johnson, trails specialist for the mountain region of North Carolina, helped me find a study trail, introduced me to key state park staff and the trail building team, and answered questions about park history. Drew Cade, Lake Crabtree County Park manager, was supportive of my project and helped me secure a research permit and determine appropriate camera locations. Thank you both for your support in making this project possible.

I would like to thank several graduate students who went above and beyond in their help with his project specifically. Kaitlin Burroughs and Tian Guo both deserve badges of honor for volunteering their time on multiple weekend trips to Stone Mountain State Park to help me move cameras and collect data. Tian, Kaitlin, Fernando Cardoso, Shuangyu Xu, Kathryn Battle, Dominique Dilandro, Moriah Boggess, and Carson Billings all braved hiking through dense shoulder-high grasses, briers, ground bee nests, mountain laurel thickets, pouring rain, and even snow to boldly navigate to the next sampling point in our forested game of connect-the-dots. I learned so much from these individuals on our trips, and I hope they had at least half the fun as I did in their company.

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A special paragraph is reserved for my husband, Fernando Cardoso, who helped me in many of the above endeavors and more. Fernando has listened to my joys and frustrations throughout my degree at NCSU. He has proofread countless papers, sat through practice presentations, and kept me fed and happy. He braved the wilds of Stone Mountain State Park with me on 11 occasions, identified animals from over 100 camera deployments, and somehow still encouraged me to finish my degree. Muito obrigada por ser tão fofo, meu amor.

I would truly like to thank my parents and sisters, who have been nothing but supportive of my wacky ideas since I started teething on box turtles. My parents graciously hosted numerous trips to Stone Mountain State Park. And finally, thank you to Douglas the Bear, who endured months of being watched in his secluded home in Stone Mountain and only ripped a camera off a tree once.

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CHAPTER 1. General Introduction

As I walk along the trail, I take in the Appalachian forest surrounding me: A pileated woodpecker laughing in the tree tops, sunlight playing on the bright green oak leaves and leathery rhododendron leaves, the smell of the earth on this well-trodden path, the snap of a twig beneath my boot, a light breeze blowing the scent of pine from the hill ahead. I see the white tails of a group of deer bounding away in the distance. I notice the footprint of a coyote, the scat of a bear, and a horse’s hoof print. Nearby, I see the impression of a hiking boot. I am not alone in this forest. Many others have also experienced these sensations in their own ways. Many creatures live in these woods, perhaps hiding only while I pass through their habitat. Or perhaps some of those creatures feel a lasting effect of my presence. Perhaps because of my presence, the next human visitors might not have the chance to see deer retreating from the trail, or maybe they will pass within feet of the deer grazing close to the trail.

Countless scholars have pondered such sensations before me. How is the environment affected by human activity? How does recreation shape the landscape, from soil erosion to wildlife communities? The study of recreation ecology is founded on such questions; it is a field in which researchers investigate the impacts of nature-based recreation and tourism on natural or semi-natural environments (Hammitt, Cole, & Monz, 2015; Liddle, 1997). Recreation ecology was established in the early 1960s in response to the global increase in recreation and tourism activities in protected areas (Wagar, 1964). This increase in nature-based recreation participation continues today (Balmford et al., 2009; Cordell, 2012; Hammitt et al., 2015). As of 2012, nature-based recreation provided 6.1 million jobs in the U.S. and resulted in nearly $650 billion in annual spending (Outdoor Industry Association, 2012). With an estimated 759 million visits to U.S. state parks alone in 2014 (Leung, Smith, & Miller, 2016), protected areas enable people to connect with nature. These social and economic contributions support the provision of recreation opportunities in protected areas.

As I continue to hike, I wonder how many people might have walked this path before me and if I will see others during my visit. Noticing horse hoof prints and bike tracks on the trail, I wonder if these two trail users passed each other amicably. I wonder why one section of the trail is muddy, while others remain dry. Protected area managers need data to answer these questions and to provide quality recreation opportunities for different user groups. Unfortunately, visitor use and impact data are typically not available (Hammitt et al., 2015), with park management resources often allocated to other efforts, such as wildlife management and infrastructure maintenance (Cole, 2006). In many cases, wildlife management in protected areas is a question of visitor management, through managing visitor access to wildlife habitat (Decker, Riley, & Siemer, 2012). These elements highlight the demand for methods to monitor wildlife and human users of protected areas simultaneously.

The trail that I hike along is my pathway through the forest. It allows me to travel through an otherwise inaccessible area, with signs pointing my way back from where I started. It allows me and other recreationists to experience the sights, sounds, and smells of the forest. This trail is also a pathway for wildlife, an edge habitat, a structure fragmenting the landscape, a vector for invasive species, and a site of soil erosion (Ballantyne, Gudes, & Pickering, 2014; Ballantyne & Pickering, 2015; Kays et al., *In Review*; Leung, 2012; Sutherland, Bussen, Plondke, Evans, & Ziegler, 2001; Wimpey & Marion, 2011). This trail is an area in which human-wildlife interactions are high (Knight & Gutzwiller, 1995), which I noticed as I observed the group of deer fleeing my presence. This pathway is a good place to observe both humans and wildlife, observations which will provide data to improve our understanding of human-wildlife interactions.

In this dissertation I seek answers to questions which have inspired recreation ecologists since the 1960s, and which have drawn the attention of wildlife ecologists in recent years. Although we have already learned a lot about human-wildlife interactions, nature-based recreation is nearly as complex as the ecosystems in which these activities take place. While experimental studies have revealed patterns of recreational impacts, such as the curvilinear relationship between use and impact on certain vegetation communities, our understanding of human-wildlife interaction is far from sufficient, especially considering the extent of nature-based recreation worldwide (Monz, Pickering, & Hadwen, 2013). In a seminal work on the effects of nature-based recreation on wildlife, Knight & Cole (1995) recognized six factors of recreational disturbances which influence wildlife responses: type of recreational activity, recreationists' behavior, impact predictability, impact frequency and magnitude, timing, and location. The non-stationary nature of animals as well as the many possible combinations of these six factors contributes towards the difficulty of detecting broad patterns regarding the impacts of recreation on wildlife.

Disturbances from human recreation have been shown to effect wildlife at individual, population, and community levels (Knight & Gutzwiller, 1995), inciting physiological responses (Gabrielsen & Smith, 1995), leading to population decline due to habitat degradation and displacement (Anderson, 1995), and altering behavior (Knight & Cole, 1991; McGowan & Simons, 2006; Whittaker & Knight, 1998). Human use areas have been identified as potential attractive ecological sink habitats for some species (Hebblewhite & Merrill, 2007; Roever, Boyce, & Stenhouse, 2008), and alter predator-prey relationships through becoming predator shelter areas (Berger, 2007; Muhly, Semeniuk, Massolo, Hickman, & Musiani, 2011; Shannon, Cordes, Hardy, Angeloni, & Crooks, 2014) and releasing mesopredators (Cove et al., 2012; Crooks & Soulé, 1999; Ordeñana et al., 2010; Prugh et al., 2009). Many previous studies investigating human-wildlife interactions in the recreation context have been observational (Hammitt et al., 2015; Monz et al., 2013), lacking the capacity of causal inference afforded by experimental designs such as the before-after control-impact (BACI) design (Beyers, 1998; Paul, 2011). With recent improvements in the technology of motion-triggered cameras (i.e. camera traps), long-term data on wildlife populations in remote settings has become more accessible (McCallum, 2013). This method lends itself to improving our understanding of human-wildlife interaction, but the efficacy of this method to quantify human activity has not yet been empirically tested.

My goal in this dissertation is to address three related research questions:

1. How effectively can motion-triggered cameras capture human trail-based activity when positioned consistent with established wildlife protocols?
2. How do trail building and trail presence affect terrestrial wildlife site use at the population level?
3. How do trail building and trail presence affect terrestrial wildlife site use at the community level?

To address these research questions I first experimentally develop a method using camera traps to capture trail-based activity and empirically test this method to determine its reliability for a range of trail user groups. I then implement this method using a BACI experimental design to determine the degree to which trail building and trail presence alter the terrestrial wildlife community in the Appalachian Mountains of North Carolina. Implementing a BACI experimental design, I am able to draw conclusions regarding the impacts of trail building both during and after the construction phase using causal inference.

Dissertation Organization

This dissertation is organized following a three-article format. It includes a general introduction (Chapter 1), three manuscripts intended for publication as peer-reviewed articles (Chapters 2 – 4), and a general conclusion (Chapter 5). Each manuscript chapter addresses one of the research questions listed above. The introduction provides context for the dissertation, illuminating the previous research on which the project is based and highlighting the need for the present research. In the conclusion I reflect on the results of the three manuscripts, drawing general conclusions and implications from the results.

As a whole, this dissertation aims to improve the tools available for quantifying human-wildlife interactions and investigates the impacts that building new trails has on terrestrial wildlife communities. By improving these tools I hope to inform and guide future studies that can more fully establish the factors influencing this complex interaction, specifically understanding how the provision of recreational opportunities affects wildlife, and how protected area managers can minimize potential impacts. I aim to provide results that will contribute to the preservation of nature-based recreation resources like those I enjoyed on my hike through the Appalachian forest, conserving biodiversity and essential ecosystem functions.

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CHAPTER 2. Camera Traps as a Method to Monitor Park Recreational Use

Abstract

The global rise in nature-based recreation brings an increasing need for research on human-wildlife interactions in protected areas. Understanding these interactions will lead to better management of protected areas, potentially improving visitor experience while also reducing impacts of recreation on wildlife. In this article we demonstrate and optimize the use of passive infrared triggered trail cameras (i.e., "camera traps") to collect data on recreational trail users. Although camera traps are now a standard tool of wildlife researchers, they are relatively new in the recreation social science field. Because study objectives differ between these fields, we predicted that field protocols for optimal camera positioning might also be different. We used a controlled experiment to determine the optimal camera position for capturing human trail users along a straight paved trail through a flat grassy area, varying only visitor movement speed and the angle and distance of the camera relative of the trail. Movement slower than 8 kph was captured by cameras significantly more often than movement at faster speeds and cameras positioned 1-2m from the trail edge and oriented 20-degrees to the line of movement captured the highest proportion of activity, regardless of target speeds. We then experimentally tested this optimal camera position in a field setting along an unpaved, multi-use trail typical of many outdoor recreation locations. Two pairs of cameras were set following our optimized protocols while two other pairs were set following a randomized control protocol. Field observers stationed within sight of the cameras recorded visitor activity to compare with the camera data. Our optimized camera traps recorded a similar number of pedestrians (82%) as our field-based observers, but detected significantly fewer mountain bikers (75%), presumably because of their faster movement speed. There was also a difference in performance of camera models, with the best camera recording 86% and 97% of pedestrians and bikers, respectively. We conclude that camera traps set for wildlife can also be used to sample human trail activity if care is taken to set cameras optimally: 1-2m from the trail, aimed at a shallow angle to the expected movement. However, it should be noted that these cameras, especially less expensive models, might under sample quickly moving visitors such as bicyclists or motorized recreationists. Thus, camera trapping has the potential to report useful data on recreationists and wildlife through a single data collection process, while providing high-resolution data useful for studying ecology, park use, and human-wildlife interactions.

Keywords: visitor use monitoring, camera trap, protected area management, recreation, trail

1. Introduction

Rising participation in nature-based recreation in the U.S. (Cordell, 2012) and globally (Balmford et al., 2009; Hammitt et al., 2015) highlights the urgency of improving our understanding of how humans and wildlife interact. Human-wildlife interactions can both influence visitors' recreation experiences and alter wildlife activity in the natural areas these species inhabit (Knight & Cole, 1991). In the United States alone, 90.1 million people participated in wildlife-associated recreation in 2011 (USFWS, 2012). Outdoor recreation activities including hiking and birding are expected to grow faster than the adult population at large by 2060, in the southern U.S. (Bowker, Askew, & Cordell, 2013). Wildlife sightings have been rated as an important part of the wilderness experience, and the lack of wildlife sightings can negatively affect the wilderness experience (Cole & Hall, 2009).

In parks and protected areas worldwide, trails are an important and common infrastructure which concentrates human movement while allowing people to travel through the landscape (Leung & Marion, 2000). High-use trails have been shown to attract some mammalian species while being avoided by others (Erb, McShea, & Guralnick, 2012). Although human-wildlife interactions have been studied widely, generalizations from this research are difficult to make due to the diversity of recreational activities, wildlife responses, study settings, and the complexity of animal movement (Kays, Crofoot, Jetz, & Wikelski, 2015; Monz et al., 2013). Fine-scale long-term data collected simultaneously on humans and wildlife is crucial in exploring these interactions, and could ultimately lead to improved conservation of wildlife species in protected areas.

Wildlife researchers have developed techniques using motion-triggered cameras (henceforth referred to as “camera traps”) to gather data on wildlife as they move past a given site (Kays & Slauson, 2008; Kays et al., 2011; McCallum, 2013; Meek et al., 2014; Rowcliffe et al., 2011; TEAM Network, 2011). Researchers interested in human-wildlife interactions have analyzed these data in relation to human use factors such as proximity to human development, intensity of recreational use, and hunting regulations (Erb et al., 2012). Although camera-based methods have also been used to monitor human trail activity for park management (Arnberger, Haider, & Brandenburg, 2005; Campbell, 2006; Duke & Quinn, 2008; Fairfax, Dowling, & Neldner, 2012), the method has rarely been employed to observe humans and wildlife simultaneously. Previous research using camera traps to observe visitors utilized substantially different study designs than those implemented in wildlife studies. In these studies cameras are typically set substantially higher off the ground and further from the center of activity than designs recommended for capturing small- to mid-sized terrestrial wildlife. Streamlining data collection on wildlife and humans through one optimized method would reduce overall monitoring costs while also providing important data related to human-wildlife interaction data. In this study we set out to develop the camera trap method to allow simultaneous observation of humans and wildlife in a trail-based setting. Using two camera models commonly employed in wildlife research, we test a range of camera positions appropriate for observing wildlife to determine the optimal camera position for gathering information on trail-based human activities and visitor demographics. We then empirically test this optimized position in a field setting to evaluate its effectiveness.

1.1 Visitor monitoring techniques

Accurate and reliable visitor data is an essential component of science-based protected area management. Recreation social scientists have developed several methods for gathering these data including field-based and remote data collection. Popular methods for remote data collection include active infrared trail counters, which record each time an infrared beam oriented across a trail is broken, and passive infrared trail counters, which record each time a temperature differential is detected (Active Living Research, 2013; Cessford & Muhar, 2003). Although trail counters are relatively easy to use and require low maintenance, this method systematically underestimates trail use due to clusters of visitors triggering the counter once, and often results in false triggers by animals or sun-warmed leaves. Additionally, trail counters deliver only a count of total trail use and do not provide information regarding trail user activity, direction of travel, or demographics (Active Living Research, 2013). Field observation has typically been implemented to gather more detailed information on visitors, including activity, direction of travel, group size (Broom & Hall, 2010), number of people at a location (Manning & Anderson, 2012), and demographics (McKenzie, Cohen, Sehgal, Williamson, & Golinelli, 2006). These data are often used primarily for park and visitor management purposes (see Cessford & Muhar, 2003). However, if combined with wildlife data, these visitor use data could be valuable in revealing fine-scale patterns in terms of human-wildlife interactions.

Since the advent of digital camera traps, several researchers have used them to collect visitor use data in protected areas. Campbell (2006) found camera traps to be a cost-effective means of gathering detailed trail use data. In that study, cameras were used to collect information on numbers of trail users, type of activity, group size, direction of travel, day vs. overnight use, and the length of time spent on the trail. The camera method was considered an improvement over trail counters, capturing activity type and minimizing the possibility of false counts triggered by animals. In another study researchers placed camera traps on human and wildlife trails to determine the intensity of human and wildlife use both spatially and temporally, finding the method to be an effective way to monitor all trail use (Duke & Quinn, 2008).

The accuracy of camera traps in capturing people or wildlife moving past them depends on two technical aspects of their performance: motion sensor sensitivity and trigger delay. Most modern camera traps use passive infrared motion sensors, which trigger when they sense changes to the temperature profile, typically due to the movement of a warm-blooded animal (Kays & Slauson, 2008). Distances over which cameras trigger depend on the camera model and the size of the animal, with larger animals triggering the sensor over a larger area (Rowcliffe et al., 2011). All digital camera traps have a delay between when the sensor detects motion and when the camera captures an image, typically ranging from 0.1-3.0 seconds (Trailcampro LLC, 2015). Fast-moving targets traveling near the camera could trigger the camera and be out of view before an image is captured. Thus, camera traps must be set close enough to trails to reliably trigger on people or animals walking along a trail, but not too close, or at too sharp an angle, to allow moving targets to exit the picture frame before an image is captured. This limitation was seen in one study that found that only 63%

of cyclists were captured on camera, while 82% of pedestrians, 90% of motor vehicles, and 100% of horses were captured (Fairfax et al., 2012). This is likely due to the speed at which users passed the cameras as well as the size of the user, with size enhanced by the use of motor vehicles and horses. Camera-based methods also yield different visitor counts from field-based observation depending on intensity of use. Arnberger et al. (2005) found that observations made from constantly recording video cameras placed at trail heads resulted in fewer single bicyclists compared with counts by field observers at low use levels, while at high use levels human observers counted fewer walkers and bikers than did video-interpreters. Thus, camera-based methods have the potential to be a useful tool in visitor monitoring, but there are limitations that must be considered when designing the study.

1.2 Contrasting camera positioning

Recreation social scientists using camera- or video-based methods to collect data on visitors have come to consensus that cameras should be calibrated before the data are used, and several sources provide guidelines for positioning cameras to capture human trail users (Arnberger et al., 2005; Campbell, 2006; Duke & Quinn, 2008; Fairfax et al., 2012). However, through our literature review we did not find any sources in which these guidelines were empirically tested. Additionally, the camera positions implemented by recreation social scientists often vary considerably from those used by wildlife researchers, as summarized in Table 2.1.

Table 2.1. Field camera positioning methods used in previous studies for visitor monitoring and mammalian studies.

	Type of camera	Height from ground	Orientation	Distance from detection zone	Tree size; other information	Citation
Human-focused studies	Passive Infrared (PIR)-triggered digital cameras	4-5m	Parallel to trail	No more than 8m from center of trail	Tree size: 30cm diameter. Facing at least 25m of trail	Fairfax et al., 2012
	PIR-triggered digital cameras: GameVue, Deercam, Reconyx	Approx. chest height	45° to trail	Not specified	Attached to trees with a minimum 6-inch (15.34cm) diameter. Tilted slightly down towards trail.	Duke & Quinn, 2008
	PIR-triggered digital cameras	Not specified	Range of angles used; optimal placement parallel to visitor movement.	Not specified	Optimal placement at a bend in the trail on level ground.	Campbell, 2006
	Time-lapse video: single images taken at 1.6-second intervals	4m	Not specified	Not specified	Placed on wooden poles or walls of buildings, concealed in nest boxes	Arnberger et al, 2005
Mammalian wildlife-focused studies	PIR-triggered digital cameras with scent lure	Knee-height (0.3-0.5m)	Parallel to slope	NA (Wildlife trails not targeted)	Not specified	Erb et al., 2012
	PIR-triggered digital cameras: Reconyx HC500, PC800	0.3-0.5m off ground; parallel to ground	Diagonal (not perpendicular) to animal travel path	2-4m from animal trail	Not specified	TEAM Network, 2011
	PIR-triggered digital cameras	0.2-0.5m for small- to medium-sized fauna; 1m for larger fauna	Discussed but not specified	Discussed but not specified	Unpublished data indicates different orientations to trail yielded significantly different detection probabilities.	Meek et al, 2014
	Variety of remotely triggered cameras (e.g. pressure-triggered, infrared motion triggered, etc)	Aimed at target animal height or lower to capture a range of animal sizes	Not specified	2-5m from midsized mammals; closer for smaller animals	Discussion of concealing cameras to avoid vandalism and theft	Kays & Slauson, 2008
	PIR-triggered digital cameras: Reconyx RC55	0.2m	Most effective detection between 15-25 degrees to camera line of sight	Most effective detection at 2-4m for larger mammals (8-25kg)	Slower and larger mammals had higher detection rates. Maximum speed detected was approximately 1 kph (30.3 cm/s)	Rowcliffe et al, 2011

One of the major differences between studies focused on quantifying human activity compared with those focused on mammalian wildlife activity is camera height in relation to the ground. While wildlife-focused studies generally place the camera approximately knee-height from the ground to capture small- to medium-sized mammals (Erb et al., 2012; Meek et al., 2014; TEAM Network, 2011), human-focused studies often place the camera higher (1.5m to 5m) (Arnberger et al., 2005; Campbell, 2006; Duke & Quinn, 2008; Fairfax et al., 2012). The recommended distance from the detection zone (i.e., the trail in the present study) also varies between visitor- and wildlife-focused studies. Wildlife researchers recommend that cameras are placed 2-5m from the detection zone (Kays & Slauson, 2008; Rowcliffe et al., 2011; TEAM Network, 2011), while visitor-focused studies recommended that cameras are placed up to 8m from the detection zone (Fairfax et al., 2012). Researchers from both disciplines generally agree than the camera should be oriented diagonally to the direction of movement (Campbell, 2006; Fairfax et al., 2012; TEAM Network, 2011).

Standardizing camera positioning could allow finer-scale research on human-wildlife interactions. The objectives of this paper are to (1) determine the optimal position of camera traps for capturing trail-based human activity and (2) test this optimal position in a field setting to determine the accuracy of cameras for quantifying a range of trail user activities and demographics. The positions tested here are consistent with those used in past wildlife studies.

2. Methods

We used a two-step process to address the project objective of developing the camera trap method for observing humans and wildlife simultaneously in a trail-based setting. We first empirically tested the percent of bicycle passes captured in photographs (i.e., capture rate) along a straight, flat, paved trail to determine the optimal camera position (Section 2.1). We then applied this optimal position in a forested trail setting to determine the reliability of camera traps in collecting data on human trail users (Section 2.2).

2.1 Optimization Study

2.1.1 Study site

The first step of the project was carried out at an athletic practice field on the campus of North Carolina State University. The location was a flat, grassy field with a paved path running along one edge. Since bicyclists have proven to be the most difficult recreationist type to capture with high accuracy in previous studies due to their speed (Fairfax et al., 2012), we tested a range of camera positions on a biker moving at a range of speeds. One of the authors biked along the paved path while another author adjusted the camera positions according to the method described below.

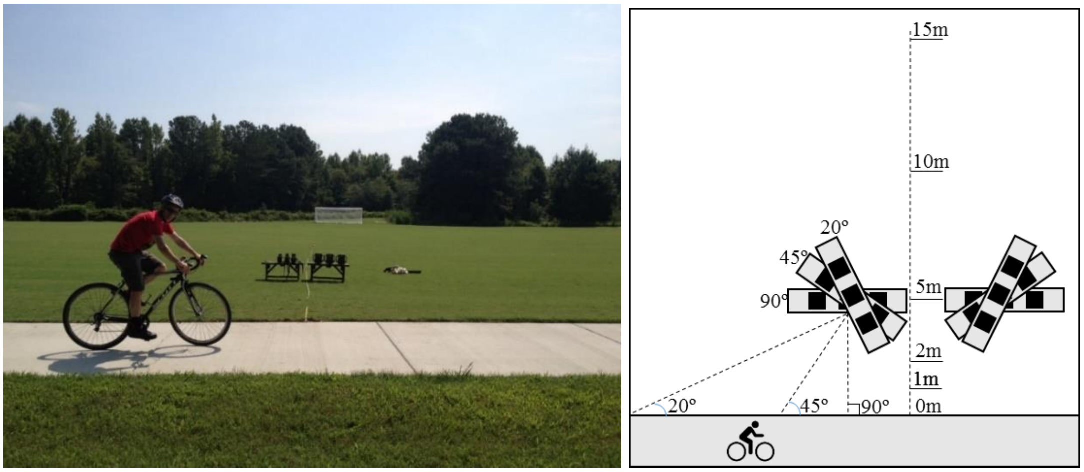


Figure 2.1. Empirical test of camera positions on the campus of North Carolina State University. Cyclist on the paved path in front of the test cameras (left). Diagram of the camera positions, including six distances from the trail edge and three angles to the direction of travel (right). Cameras are indicated by black boxes, and were placed on benches indicated by grey rectangles (diagram not to scale).

2.1.2 Procedures

We used three Bushnell Trophycam HD cameras and three Reconyx Rapidfire cameras to take three photographs per trigger. The cameras were placed on benches 0.5m off the ground set at a range of distances (0, 1, 2, 5, 10, and 15m) from the trail edge (Figure 2.1). At each distance, the cameras were tested at three orientations to the trail: 20, 45, and 90 degrees. One of the authors biked along the trail three times at four different speeds (5, 10, 15, and 20 miles per hour, equivalent to 8, 16, 24, and 32 kilometers per hour) for each combination of distance, angle, and direction relative to the camera. Some distance-angle combinations (e.g., 20 degrees at 15m) produced no photographs, showing that the trail was out of range of the cameras at such positions. Manufacturers report a trigger speed (delay between a motion trigger and the capture of an image) of 0.6s for the Bushnell Trophycam HD and 0.2 seconds for the Reconyx Rapidfire (Bushnell, 2012; Reconyx, 2009). All cameras were set to the lowest picture resolution available (3 megapixels) to minimize the time required to write the image to the memory card. Cameras were set to have a one second lag time between triggers to standardize the results from the two models. These two camera models were chosen to represent a relatively low and high price ranges. Bushnell Trophycams were purchased for less than $200 while the Reconyx cameras typically range from $450-$650.

Test photos were analyzed to determine the combinations of speed, angle, and distance which were most successful in capturing a photo of the biker. During analysis we found that one camera was not functioning due to low batteries. This camera was omitted from the analysis, leaving three Bushnell and two Reconyx cameras in the analysis. By examining descriptive statistics we determined the camera positions with the highest rate of capture, expressed as the percent of passes, which resulted in a photo of the biker. Based on these results we determined an optimal range of positions for counting trail users and capturing activity type and demographic information on these individuals.

2.2 Field trials

2.2.1 Study site

The second step of this project was conducted at Lake Crabtree County Park in Morrisville, North Carolina (Figure 2.2). The study trail is designated for mountain bike use and open to foot traffic and on-leash dogs as well. The area is forested and located in a suburban zone, 18km from the city center of Raleigh, NC. The trail studied is part of the mountain bike trail system within the park and is often used as a connector trail with a nearby state park. Field-based data collectors were trained and an inter-rater reliability test was conducted along a greenway on the campus of North Carolina State University.

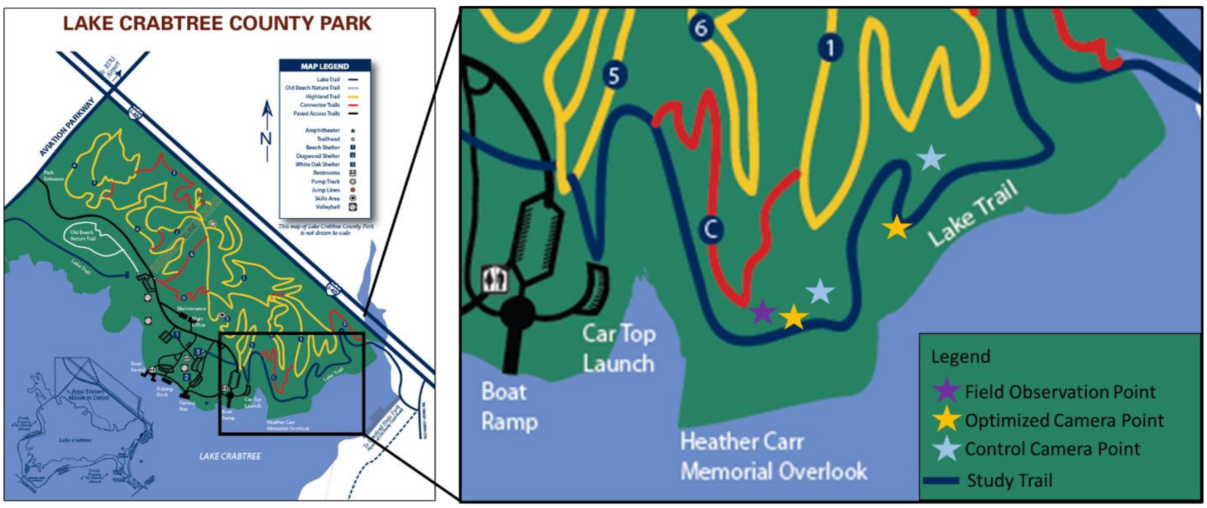


Figure 2.2. Map of Lake Crabtree County Park with locations of the observation points, indicated by stars. Map adapted from official park map (Wake County, 2015).

2.2.2 Procedures

In the second step of this research project we tested the optimized camera position from the results obtained from the optimization study in a less controlled setting, on an unpaved trail in a public park with varied topography, trees, and recreationists. To reduce the known problem of camera traps missing quickly moving cyclists we selected two points (Point 1 and Point 2) where mountain bikers were expected to travel relatively slowly due to tight turns, exposed roots, and steep inclines. At these points we set one of each type of camera (Bushnell and Reconyx) at a distance of 1-2m from the trail edge and an angle of 20 degrees towards the trail. These were considered “optimized” points based on our previous tests. Two paired control points were selected at a random distance of 10-30m from the optimized point along the trail. The orientation and distance from the trail were randomly selected within the parameters tested in the optimization study. Control positions did not match those positions that resulted in a high capture rate in the first part of the project. One camera from each manufacturer was set at the randomized angle and distance from the trail at these points. Position details are shown in Table 2.2. With one Bushnell and one Reconyx camera at each optimized and control point, a total of eight cameras were used in this part of the project. All cameras were set to take three 3-megapixel photos per trigger, with a lag time of one second between triggers. Cameras were run for 16 days, with three field observation sessions conducted during weekend afternoons.

Table 2.2. Position details for optimized and control points in Step II. Detection distance indicates the distance at which the camera’s passive infrared (PIR) trigger is activated, observed through a flashing light in setup mode.

	Treatment	Angle to Trail	Distance from Trail Edge (m)	Detection Distance (m)	
				Bushnell	**Reconyx**
Point 1	**Optimized**	20°	1	15	16
	Control	90°	3.5	6.5	7.5
Point 2	**Optimized**	25°	1	15	20
	Control	30°	9	20	18

To quantify the proportion of people captured by the camera traps we conducted three observations of the site in front of cameras in the field, with observers stationed within sight of Point 1. Field observers recorded each time a person passed the camera at Point 1. No field observation was made at Point 2; since there were no intersections between the two points, it is assumed that each person observed at Point 1 also passed Point 2. Each observation included the time, direction of travel, activity (bike, walk, run, other), sex (male/female), age group (youth: 0-13 years old, teen: 14-20, adult: 21-59, senior: 60+), and race category (White, Black, Hispanic, Asian, other/unknown). Demographic categories were modelled after the "System for Observing Play and Recreation in Communities" (SOPARC) method (McKenzie et al., 2006). For bikers, the presence of a helmet was noted, and the use of a leash was noted for dog walkers. All observations were made on weekend afternoons in November 2014, to correspond with high-use periods for the study trail.

Each camera trap was used to document trail use through photo analyses, counting the number of times an individual passed the camera. Data were extracted from photos taken and stored in Microsoft Excel. Descriptive statistics were conducted using Microsoft Excel, and statistical analyses were performed using Statistical Package for the Social Sciences (SPSS 22) (IBM Corp., 2013) and R Version 2.13.0 (R Core Team, 2013). Inter-rater reliability among observers was tested using Cohen's Kappa (Cohen, 1960). Results from the controlled test on the campus of NCSU were compared using ANOVA and a post-hoc Tukey test.

In the field implementation at Lake Crabtree County Park, we compared overall counts of human trail use obtained from cameras were compared to those collected by field observers. We conducted paired sample t-tests to detect differences in means of observations made from each optimized camera compared with field observations. Separating all data from the field implementation into fourteen observation periods of approximately 30 minutes each, we fit data to a linear model to compare the slope and fit of each camera with the field-based observation. Counts of each activity type were compared between sample points, camera models, and treatments using chi-squared analysis. We tested for significance using an alpha level of 0.05.

3. Results

3.1 Determining the optimized camera position

The first goal of this research was to determine the capture rate of each camera type at a range of angles to the trail, distances from the trail edge, and speeds of bike passes. Figure 2.3 shows the average number of observations made from each camera model at the range of biker speeds, camera orientations, and distances from the trail tested. One-way ANOVAs indicated differences between average observations for each variable for both camera models. Post-hoc testing with the Tukey test indicated that biker passes made at 8 kph (5 mph) were captured significantly more than were passes made at faster speeds ($p<0.05$) for both camera models. Speeds exceeding 8 kph did not result in significantly different observations. Regarding the angle, both Reconyx and Bushnell cameras oriented 20-degrees to the trail captured significantly more biker passes than did those 90-degrees ($p<0.05$). Bushnell cameras oriented at both 45-degrees also captured significantly more biker passes than did those set at 90-degrees. Regarding the distance of cameras from the trail edge, observations made from Reconyx cameras placed 2m from the trail made significantly more observations than those made at all other distances tested, and cameras placed at 1m captured more activity than those at 10 and 15m. Bushnell cameras placed 5m from the trail captured significantly more observations than those placed 15m from the trail. There were no significant differences between other placements ($p>0.05$). The average of both cameras resulted in a significantly higher number of observations made at 2m than at 10 and 15m.

Analyzing the percent of passes captured for each distance-angle-speed combination, results showed that slower movement (8 kph) resulted in reliable captures over a wider range of settings, while increasing speeds decreased the likelihood of detection for nearly all distance-angle combinations. Three settings had perfect detection when the biker moved at 8 kph: cameras positioned at a distance of 0m and 1m from the trail edge, oriented 20-degrees to the trail and cameras set 15m from the trail edge oriented 90-degrees to the trail. Several other positions also had high capture rates for 8 kph passes: when the camera was oriented 20-degrees to the trail and placed 2m from the trail edge (capture rate = 87%) as well as the combinations of 45-degrees and 2m (capture rate = 87%), 5m (capture rate = 83%) and 10m (capture rate = 90%).

Speeds exceeding 8 kph were only detected by cameras placed further from the trail and/or with a shallower angle, thus giving a wider field of view to capture an image of the biker given the trigger delay. For passes at 16 kph, we found two peaks of approximately 60% capture rate: one at 1-2m from the trail edge at the 20-degree orientation and the other at 15m from the trail edge at the 90-degree orientation. The highest speeds were best captured by cameras set at a 20-degree angle and placed 2m from the trail edge, though with low capture rates (24 kph/15 mph: 37%; 32 kph/20 mph: 27%).

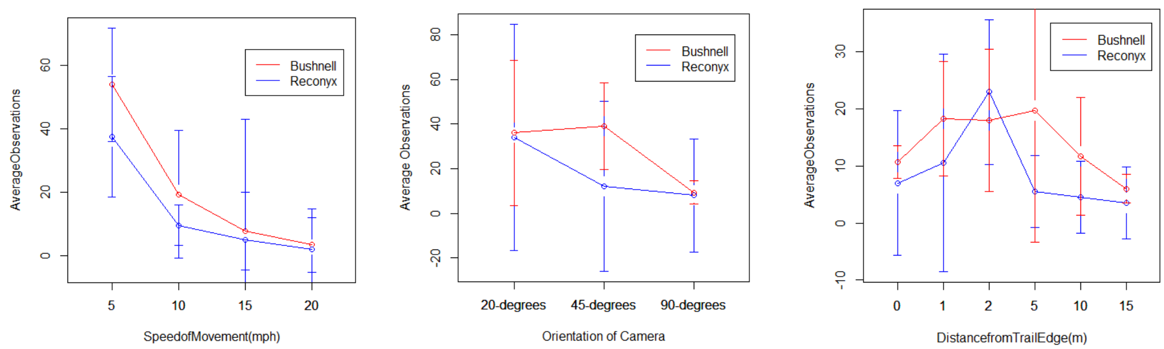


Figure 2.3. Average number of observations with 95% confidence interval for each camera model at a range of biker speeds (left), camera orientations towards the trail (middle), and distances from the trail edge (right).

Clearly, the cameras set at 20 degrees to the trail and 1-2m from the trail edge would have an optimal rate of capturing bikers moving at all speeds, a factor which is ultimately difficult to control in a field setting. Thus we considered this as an “optimal” position. Although there were other high-scoring positions, we chose this position because our test cameras scored high in both the 8 and 16 kph trials. Additionally, cameras positioned closer to the trail were expected to record images with more accurate demographic data, addressing another project objective.

3.2 Case study at Lake Crabtree County Park

3.2.1 Total observations

In the second part of this project, we applied the selected optimized camera position in a field setting at Lake Crabtree County Park. Photographic data collected during field observation sessions yielded nearly eight hours of observation at each point, with a total of 1,293 photos taken by all eight cameras. Of the photos, 1,051 indicated observations of individuals on the trail. Field observers recorded a total of 252 trail users during the eight-hour observation period. These trail users were recreationists not otherwise involved in the study and remained anonymous according to privacy agreements.

When averaged, optimized and control camera results were significantly lower than field observations ($p<0.05$). Separating each camera by treatment, manufacturer, and point, results from optimized Reconyx cameras were not significantly different from field observations ($p>0.05$), while the two optimized Bushnell cameras were ($p<0.05$). Linear regression of optimized camera-based observations compared with field-based observations indicated slopes ranging from 0.3419 (Bushnell camera, Point 2) to 0.9851 (Reconyx camera, Point 1). R-squared values ranged from 0.4635 to 0.9939 (Table 2.3 and Figure 2.4).

Table 2.3. Results of paired-sample t-test and linear model for observations made from each camera compared with the field observation. For p-values, *** indicates significance at p<0.0001, ** p<0.01, *p<0.05 levels.

Optimized Camera Point and Model	Total Observations	Paired sample t-test	Linear Model			
		p-value	R-squared	Estimate	Std. Error	p-value
Field	252	NA	NA	NA	NA	NA
Point 1 Bushnell	202	*	0.7816	0.6892	0.1052	***
Point 1 Reconyx	247	0.1365	0.9939	0.9851	0.0224	***
Point 2 Bushnell	103	***	0.4635	0.3419	0.1062	**
Point 2 Reconyx	231	0.0658	0.9407	0.8473	0.0614	***
Optimized	195.75	***	0.9464	0.7159	0.0492	***
Control	72.25	***	0.6386	0.2674	0.0581	***

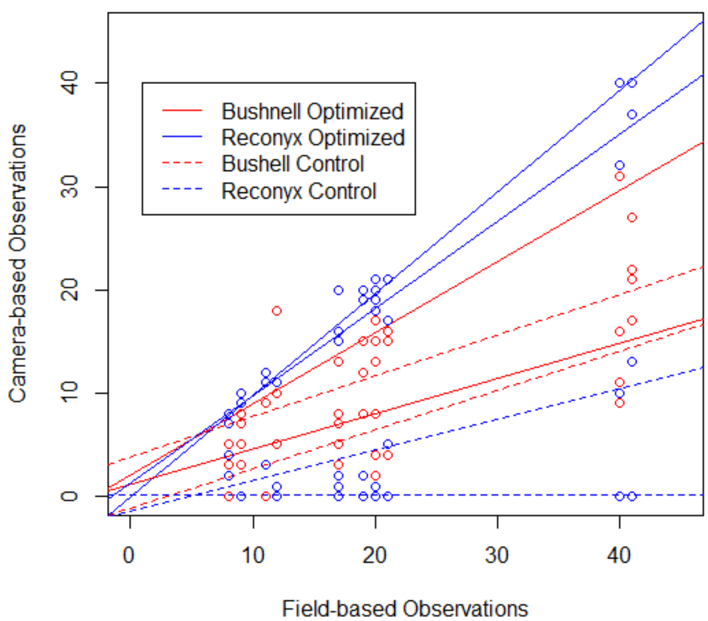


Figure 2.4. Linear model describing the total number of observations made per 30-minute period by optimized (solid) and control (dashed) cameras compared to total human passes noted by human observers. Bushnell cameras are indicated in red while Reconyx cameras are blue.

We found three general trends in the data: (1) optimized cameras generally had higher agreement with field observations than did control cameras; (2) optimized Reconyx cameras had higher agreement with field observations than did optimized Bushnell cameras; (3) there was a proportionally smaller gap between optimized and control treatments in Bushnell cameras than in Reconyx cameras.

The inter-rater reliability test resulted in an “almost perfect” agreement between field observers in terms of activity type and sex categories (minimum Cohen’s Kappa coefficient values of 0.800 and 0.939, respectively), and substantial agreement regarding race (minimum of 0.653). However, the age category had considerably lower agreement. Results from the inter-rater reliability tests, performed in two sessions, are shown in Table 2.4. Strength of agreement is interpreted according to Landis and Koch (1977).

Table 2.4. Inter-rater reliability by variable, expressed in Cohen’s Kappa

Variable	**Cohen’s Kappa**	**N**	**Strength of Agreement**
Activity	0.8	40	Substantial to Almost Perfect
	0.927	33	
Sex	0.939	33	Almost Perfect
	1.000	35	
Age	-0.062	34	Poor to Fair
	0.333	33	
Race	0.653	33	Substantial
	0.878	35	

3.2.2 Observations by activity type

We analyzed visitor observations by activity type for optimized cameras. Most field observations made were of bikers along the trail (n=185), followed by walkers (n=52), and finally runners (n=15). On average, all optimized cameras captured 81% of walkers observed in the field, 85% of runners, and 75% of mountain bikers. Due to the low sample size for runners, we grouped walkers and runners together as pedestrians for further analysis. A chi-square test indicated significant differences for both activities between sample points, so we proceeded with analysis on data from each point separately. For bikers, the number of field observations was significantly higher than the averaged observations from optimized cameras at both sample points. Pedestrian observations made from Point 1 cameras were consistent with field observations (p=0.84) while those made at Point 2 were significantly fewer than field observations.

We further analyzed differences between field and camera observations at both optimized points by camera manufacturer. For Reconyx cameras, there was no difference between the averaged camera-based observations and field observations for bikers (p=0.69) or pedestrians (p=0.38). Bushnell cameras captured significantly fewer bikers, while there was no difference between Bushnell camera observations and field observations for pedestrians (p=0.14). Figure 2.4 shows the percent of field observations captured by optimized cameras of bikers (black) and pedestrians (light gray) by camera manufacturer. Average observations and p-values from chi-square tests are shown in Table 2.5.

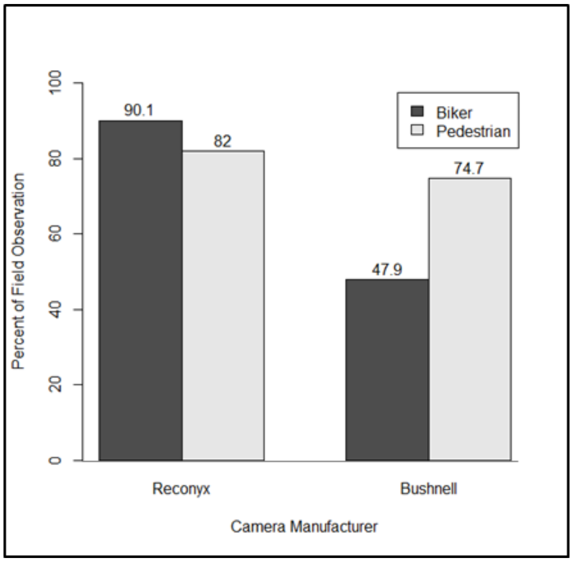


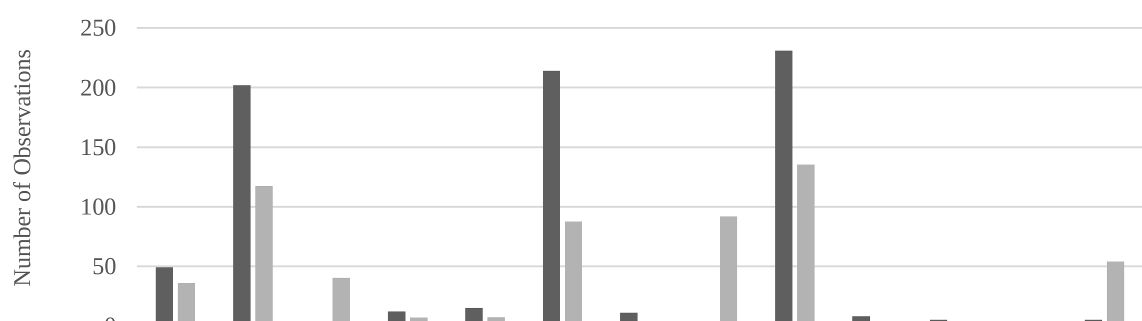
Figure 2.5. Average total captures made from optimized cameras as a percent of observations made by field-based observers.

Table 2.5. Observations for each treatment, averaged by observation point and camera model, by activity type. P-values resulted from a chi-square test comparing the treatment with the field observation for both activity categories. For p-values, *** indicates significance at p<0.0001, ** p<0.01, *p<0.05 levels.

	n	Bikers		Pedestrians	
Treatment		**Average Observation**	**p-value**	**Average Observation**	**p-value**
Field Observer	1	185	NA	67	NA
All Optimized	4	139	***	55	0.2417
Difference between Points	4	NA	***	NA	**
Point 1	2	158	*	64	0.839
Point 2	2	120	***	45	*
Reconyx Optimized	2	180	0.690	58	0.380
Bushnell Optimized	2	98	***	52	0.142

3.2.3 Demographics

Our demographic information for trail users (gathered from both optimized and control cameras) varied substantially from that collected by field observers. Due to the small sample size for some groups, significance testing was not performed. Figure 2.6 shows observations from optimized and control datasets as a percent of field observations. Observations made from optimized cameras were proportionally closer to field-based observations than were observations made from control cameras for all three types of demographic data collected. For sex and age group, the "unknown" category was not an option on the field data sheet but was necessary when processing photographs. This may explain some of the lack of agreement of the camera-based data with the field data.



	Sex			Age Group				Race				
	Female	Male	Unkn.	Youth	Teen	Adult	Senior	Unkn. Age	White	Black	Asian	Hisp.	Other/ Unkn.
■ Field	49	202	1	12	15	214	11	0	231	8	5	3	5
■ Optimized	36	117.5	40.25	7	7.25	87.5	0.25	91.75	135.25	3.5	1	0	54

■ Field ■ Optimized

Figure 2.6. Observations of demographics (sex, age group, and race) observed by field observers (black bars) and optimized cameras, averaged (grey bars).

4. Discussion

This study demonstrates the importance of camera position for detecting human trail use and shows that human activity can be accurately quantified using camera positions typical of wildlife studies. We offer the first empirical test of camera settings for capturing human trail use, concluding that the optimized camera position for recording people and animals included three criteria: (1) points where trail users are likely to be moving slowly, (2) cameras oriented 20-degrees to the trail, and (3) positioned 1-2m from the trail edge. This position is similar to zoology guidelines recommending to orient cameras diagonally or nearly parallel to recreational trails (Campbell, 2006; Fairfax et al., 2012) and wildlife trails (Meek et al., 2014; TEAM Network, 2011) and at a distance of 2-5m from wildlife trails (R. Kays & Slauson, 2008; TEAM Network, 2011).

When we applied the optimized camera positions along a mountain bike trail we found that optimized cameras captured a higher percentage of overall trail activity than did control cameras, confirming the importance of camera positioning in capturing human trail-based activity. The two camera models varied in the proportional gap between optimized and control treatments, suggesting that this positioning is more critical for the Reconyx Rapidfire camera than for the Bushnell Trophcam. The optimized Bushnell cameras also missed more trail activity than did optimized Reconyx cameras overall, showing that camera model type can affect results. When using the optimized camera settings, Reconyx-based observations did not vary significantly from field-based observations for both activity types, while Bushnell cameras captured significantly fewer cyclists. This finding is supported by previous studies which found variation among camera models, and shows the importance of trigger speed and sensitivity for camera data accuracy (e.g. Rovero, Zimmermann, Berzi, & Meek, 2013).

The proportional agreement of camera-based observations with field-based observations for each activity type was similar to that found by Fairfax et al. (2012), who used infra-red sensors combined with digital cameras at a height of 4-5m to detect trail users. The same pattern of decreasing detection rate with increasing speed was found in this study. Since our optimized camera trap position resulted in capture rates consistent with this previous study, while implementing camera setting guidelines used in wildlife research, we suggest that our camera trap method is a valid way to quantify overall human and wildlife trail use simultaneously.

Regarding speed, we found that cameras did poorly at capturing photographs of movement faster than 8 kph (5 mph). Hikers generally move at 3-5 kph, trail runners can range from approximately 5-13 kph, and mountain bikers have reported speeds up to 56 kph and averaging at 40 kph on some trails (Strava, 2016). Rowcliffe et al. (2011) demonstrated that the maximum speed of mammals recorded by cameras in Panama was less than 1 kph, and thus are probably recorded more accurately by camera traps than human recreationists.

Regarding visitor demographics, camera-based observations differed from field observations. Individual characteristics were difficult to discern in some pictures, partially due to the low resolution settings (3-megapixel) used here, and because the low settings of our cameras often failed to record people's faces. Higher resolution images could make demographic information easier to extract from photos that do include visitors' faces, but might be undesirable for privacy reasons. However, demographics recorded from photographs followed the same general pattern as did field observations, indicating that calibration using field-based observations might yield reliable trail user demographic data.

While this research demonstrated that camera traps can provide accurate data on trail user numbers and activity types, the documented method does have limitations. As shown here, the position of the camera relative to the trail is critical when attempting to gather accurate use data. Camera trap approaches also require time-consuming analyses of photographs, while other approaches (e.g., simple trail counters) do not. Open-source software has been developed for extracting data for wildlife studies, which can be adapted for visitor monitoring projects (Sundaresan, Rginos, & Abelson, 2011; Tobler, 2012). Freely available software such as Picasa and F-spot have also been used for camera trap data management (Ivan & Newkirk, 2016; Sundaresan et al., 2011).

Privacy and vandalism are often concerns when using cameras to observe humans in public areas. The optimal camera position tested in the second part of this project was visible to trail users, since cameras were located close to the trail edge. In settings where vandalism and/or theft are a concern, cameras may need to be concealed or placed in less obvious locations (see Arnberger et al., 2005), although cameras set in similar situations across 32 parks in the Eastern U.S. had few theft problems (McShea, Forrester, Costello, He, & Kays, 2016; R. Kays, personal communication, October 30, 2015). Although there are no laws against taking photographs of people in public lands in the U.S., privacy of park visitors can be respected by using low-resolution images, having off-site personnel analyze photos, posting a notice informing visitors of the use of trail cameras (Arnberger et al., 2005), or by blurring identifying features of people in any photos used beyond the immediate purposes of the primary research. Compared with chest-height (or higher) cameras used previously for human visitor monitoring, placing cameras at knee-height decreases the possibility of recognizing individuals in photos, since many photos do not capture the face.

5. Implications and Conclusions

This study demonstrates that camera traps can be used to collect accurate data on human trail users using camera settings widely used in wildlife research. Careful consideration regarding camera position is required for accurate visitor use data. Our empirical tests show that the optimal camera position is 1-2m from the trail edge, oriented 20 degrees towards a location where trail users move relatively slowly, with the highest capture rate for visitors moving 8 kph or less.

Cameras can be used to effectively record trail user activity type. Collecting reliable demographic data on trail users could also be possible by using camera traps, but how to best employ this method should be further refined through future studies. In this paper we empirically tested methods used in previous literature and found that our results agree with guidelines recommended by wildlife researchers and recreation social scientists. Researchers may also be able to use cameras to detect changes in trail conditions over time (i.e., exposed roots, bare ground, or muddy conditions). Combining trail condition changes with shifts in trail user groups attained through observational methods such as camera traps could reveal patterns in user preferences on a fine temporal scale.

One model of each of two major camera trap brands was used in this study to represent two price ranges. We found significant differences between the brands in detecting the total number of visitors and total mountain bikers. The difference in trigger time between the two cameras examined may account for some of the variation in the number of quickly moving mountain bikers recorded. Camera trap technology continues to improve, offering shorter trigger speeds and recovery times.

Protected area managers can use camera trap approaches to document the amount of use a trail receives from different user groups. Cameras can also document compliance rates in terms of issues such as compliance with dog leash rules or bike helmet regulations.

Researchers studying human-wildlife interactions can use the proposed optimized camera trap method to gather data on human and wildlife activity along trails. Previous human-wildlife interaction studies using camera trap data required external metrics of anthropogenic influences such as land use regulations, often lacking fine-scale temporal and/or spatial information. The method presented here validates the use of camera traps, a method increasingly used in wildlife research, to gather data on humans and wildlife simultaneously, paving the way for long-term research on human-wildlife interaction with high resolution temporal and spatial elements.

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CHAPTER 3. Evaluating the Impacts of Trail Building on Wildlife: A Before-After Control-Impact Experiment Using Camera Traps

Abstract

Protected areas frequently have the dual goals of conserving natural resources while providing recreation opportunities to the public. Wildlife preservation is central to conserving natural ecosystems and is an important social and economic resource in protected areas. Trail-based recreation is common in protected areas, and recreational trails provide an infrastructure for visitors to travel through wildlife habitat. However, there is concern that this infrastructure could affect the quality of wildlife habitat by bringing more people into secluded areas, and thus disturbing animals. In this study we used an experimental design to investigate the impacts of new hiking trail construction on six terrestrial vertebrate species: white-tailed deer (*Odocoileus virginianus*), eastern gray squirrel (*Sciurus carolinensis*), northern raccoon (*Procyon lotor*), coyote (*Canis latrans*), wild turkey (*Meleagris gallopavo*), and Virginia opossum (*Didelphis virginiana*). Using motion-triggered cameras (camera traps), we monitored animal use of the study area before, during, and after construction over one year at three sites: along the trail, near the trail, and at a control site. Through zero-inflated Poisson regression and occupancy analyses we found statistically significant impacts of trail building and trail presence on four species. During the motorized construction of this approximately 2-m wide equestrian trail, deer decreased their use of the near-trail sites and coyotes decreased their activity at and near the trail. Both species returned to the area at pre-building rates once trail construction was complete. Raccoons showed increased use along

the trail during construction. Squirrels were the only species which showed a significant change in habitat use after trail building was complete, showing decreased use along the trail itself, but not in the near-trail sites. We conclude that while trail building has impacts on the habitat quality for some species, these mostly occur during the trail building phase. To further minimize these impacts, we suggest that trail building should be restricted to a short time period in which species of concern are least sensitive, especially where endangered species are present. Our study demonstrates that recreation and wildlife can coexist and are not in conflict.

Keywords: wildlife, trail, recreation, before-after control-impact, experiment, camera trap, occupancy

1. **Introduction**

Protected areas are set aside from development to preserve natural ecosystems. Most of these areas also provide recreation opportunities. While providing these opportunities in natural settings is an important role of many protected areas, human activities associated with recreation can alter ecosystems both locally and beyond protected area boundaries (Knight & Cole, 1991; Liddle, 1997).

Trails are a key infrastructure for recreation. The percentage of protected area visitors that use trails is high worldwide (60% to 87%) and varies with trail quality (Blotkamp, Meldrum, Morse, & Hollenhorst, 2010; Department for Environment and Heritage, 2008; Reed et al., 2008). Nearly every protected area has trails; even areas classified as "Strict Nature Reserves" by the International Union for the Conservation of Nature contain this infrastructure (Dudley, 2008). Recreation trails continue to be built, maintained, and re-routed in nature conservation areas. For example, trail mileage in U.S. state and federal lands increased by 43% between 1965 and 2015, a total increase of over 214,500 kilometers of trails (American Hiking Society, 2015). Although interactions of humans and wildlife have been studied along recreation trails, few studies have investigated in the impact of trail construction on wildlife.

Past research has shown species-specific effects of the trail structure on terrestrial wildlife species with some species preferring to use human trails while others avoid them. Large carnivores and predators such as felids and canids prefer to use trails (Cusack et al., 2015; Harmsen, Foster, Silver, Ostro, & Doncaster, 2010; Karanth & Nichols, 1998, Kays et al., 2011) while species such as martens, fishers, weasels, and raccoons are not expected to disproportionately use trails (Gompper et al., 2006), and prey species sometimes avoid trails (Kays et al., 2011). Human recreation activity also leads to a range of responses in terrestrial vertebrates, and can create attractive sinks (attractive habitat patches with low survival or recruitment) and human-shielded predator shelter zones (Berger, 2007; Hebblewhite & Merrill, 2007; Muhly et al., 2011; Roever et al., 2008; Shannon et al., 2014). In the Appalachian Mountains, black bears (*Ursus americanus*) were found to avoid high-use trail areas while red foxes (*Vulpes vulpes*) were attracted to these areas (Erb et al., 2012). In a review of the impacts of a range of recreational activities on ungulates, Stankowich (2008) reported that ungulate populations in areas with higher levels of human activity showed reduced wariness. Further, bird nests near trails have higher success rates than those further from trails (Miller & Hobbs, 2000). A trail structure could lead to an altered predator-prey balance in the long-term, even if human use is very low.

Most studies of human-wildlife interaction in natural settings rely on correlational designs to test hypotheses, and thus have limited ability to infer causation. Experimental design has been used in several road building impact assessments as well as two studies on the impact of building a bike path parallel to an existing road in Grand Teton National Park (Chalfoun, 2011; Shannon et al., 2014). In this area, a change in behaviors of two ungulate species was observed following the construction of the bike path. Specifically, ungulates exhibited behavior associated with reduced predatory threat near the paved path after it was built compared with previously (Shannon et al., 2014). Breeding birds showed avoidance of the new path area, but bird nests near the path had increased success rates (Chalfoun, 2011). These findings show strong evidence for the human shield hypothesis (Berger, 2007; Muhly et al., 2011), with both predator and prey species exhibiting altered habitat use after the construction of a recreation trail as compared with before construction. However, the majority of human-wildlife interaction studies do not include all elements of a controlled experiment. Through a before-after control-impact (BACI) experimental design, researchers can draw stronger conclusions on the relationship between tested variables using causal inference.

In this study we conducted a BACI experiment to investigate the impacts of trail building on terrestrial vertebrates. We addressed the research question: how does motorized trail building and the presence of a new trail affect six terrestrial vertebrate species at the population level? The target species we investigated included five mammals and one large ground-dwelling bird: white-tailed deer (*Odocoileus virginianus*), eastern gray squirrel (*Sciurus carolinensis*), northern raccoon (*Procyon lotor*), coyote (*Canis latrans*), Virginia opossum (*Didelphis virginiana*), and wild turkey (*Meleagris gallopavo*), henceforth referred to as deer, squirrel, raccoon, coyote, opossum, and turkey. In answering our research question, we aimed to identify patterns in species' reactions to trail construction and the recreational trail structure which might apply to trail construction or improvement projects in other regions.

2. Methods

2.1 Study site

This study took place in Stone Mountain State Park, North Carolina, located in the foothills of the Appalachian Mountains. This 57-km^2 park is in a rural area and contained occupied homesteads until the late 1960s, when it was designated as a state park. The study trail is a 2-m wide equestrian trail that was built using motorized machinery from February 6th through June 5th, 2015, and opened to recreational use on June 6th, 2015. Trail design and building were carried out in accordance with the International Mountain Biking Association (IMBA) sustainable trail building guidelines (see Felton, 2004), a set of guidelines widely used in the sustainable design of a variety of recreational trail types. The study trail is located at a minimum distance of 275m from existing trails and 460m from existing roads or other park infrastructure. Both treatment and control sites have abandoned logging roads and a power line running through them. The logging road in the treatment zone was used as an equestrian trail until 2008. The trail zone is classified as Eastern North American Cool Temperate Forest, dominated by Southern and Central Appalachian Oak Forest (USGS, 2014), at elevations ranging from 463 to 578m above sea level (NC OneMap, 2014). The control site is located in an area with a similar ecosystem, distance to existing trails and roads, and elevations ranging from 454 to 628m above sea level. No hunting is permitted within the park.

2.2 Study design

Data were collected during three phases: before trail building (August 30th, 2014 – February 5th, 2015), during trail building (February 6th – June 5th, 2015), and after the trail was completed and open to recreational use (June 6th – September 12th, 2015). Twenty-one sampling points were located in each of three zones: (1) along the study trail, (2) in a near-trail corridor located 25-50m on either side of the study trail, and (3) in a control site. On-trail sampling points were randomly selected at a minimum interval of 124m along a 2600m section of the proposed trail, which was previously delineated with markers at the site and mapped using a Global Positioning System (GPS) unit. Near-trail sample points were determined by drawing a line perpendicular to the trail at each on-trail point, an then placing a point on a randomly selected side and distance from the trail within the 25 to 50m near-trail zone. Slight alterations were made to this randomization process to ensure that each point was located at an appropriate slope and minimum distance of 25m from all sections of the trail, specifically in sections where the trail contains multiple switchbacks.

The control site was determined using topographic, geologic (NC OneMap, 2014), vegetation (USGS, 2014), and park infrastructure and boundary maps (unpublished data provided by the NC Department of Parks and Recreation) using ArcMap 10.1, and located at a distance of approximately 2.5km from the study trail. In the control site a 2600m line was drawn to reflect the slope and elevation range of the study trail. Control site sampling points were determined along this line using the same method as the on-trail sampling points. A map of the study site, including insets of the control and treatment areas, is provided in Figure 3.1.

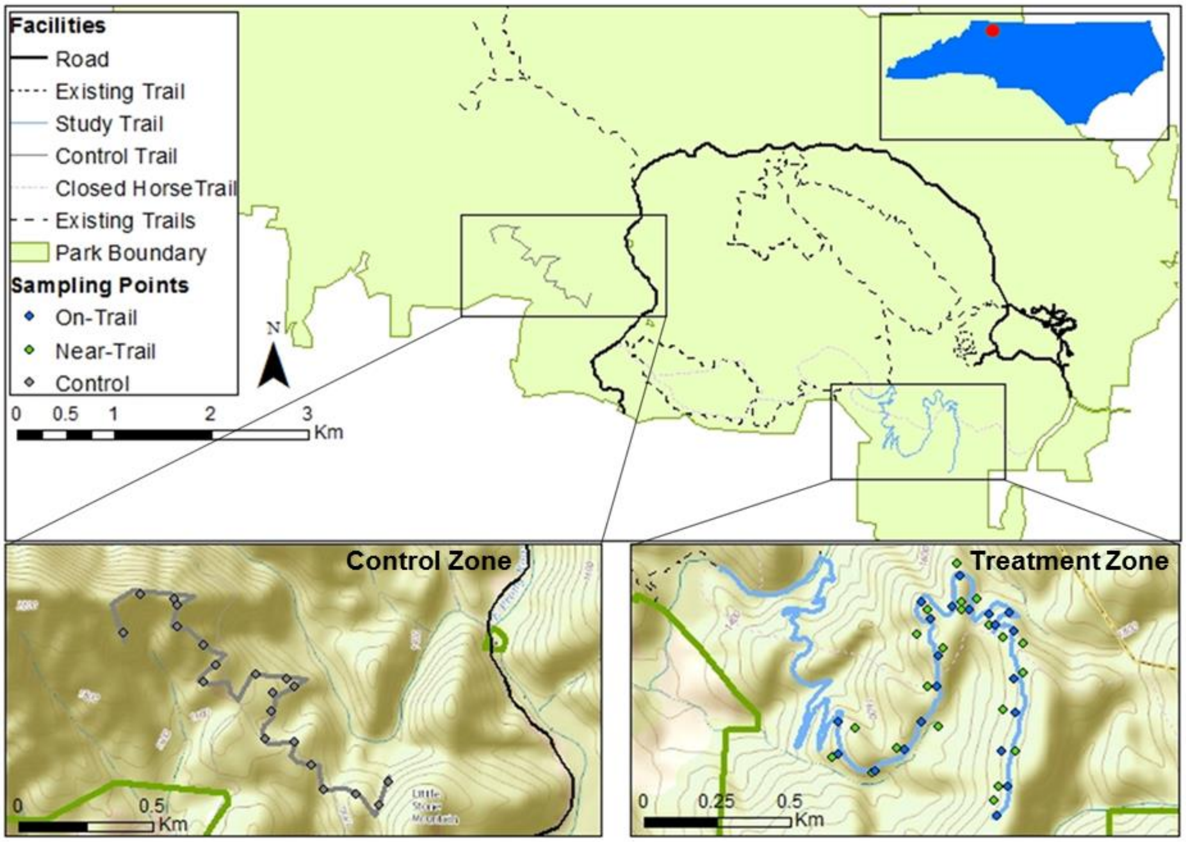

Figure 3.1. Map of the study site in the southern portion of Stone Mountain State Park. Sampling point locations are marked in insets: control zone (left) and treatment zone (right). Location of the park within North Carolina is indicated with the red point in the inset in the top right corner.

2.3 Data collection

All field data were collected using motion-triggered field cameras, henceforth referred to as camera traps, a widely used and relatively non-invasive method in wildlife studies (Kays et al., 2011). Cameras used in the study were Bushnell TrophyCam HD, a budget camera which is considered suitable in wildlife monitoring (Rovero et al., 2013). At each sampling point, a camera was attached to the nearest tree of appropriate size at knee-height from the ground (approximately 0.5m). Cameras were oriented towards an open area with a relatively flat slope, with lenses angled parallel to the slope of the ground. In rare occurrences, nearby vegetation or underbrush was cleared to improve camera performance. On-trail cameras were oriented along the trail to maximize the trail-based activity detected (Chapter 2). These procedures are typical for studies using camera traps for wildlife data collection (e.g. Erb, McShea, & Guralnick, 2012; Meek et al., 2014; Rowcliffe et al., 2011; TEAM Network, 2011).

A total of twenty-one cameras were used for the study, divided evenly between the three study zones. Seven cameras were deployed in each study zone for a period of three weeks, at sampling points spaced at approximately 370m along the trail. After typically three weeks (range: 19-38 days, mean: 23.5 days), we exchanged memory cards and batteries and moved each camera to the next sampling point, allowing all twenty-one points in each zone to be sampled in a total of nine weeks.

Cameras were programmed to take three photographs per trigger with a delay of one second between trigger events and no delay between retriggering. Photos were aggregated into sequences separated by at least one minute between camera triggers to minimize repeated observations of the same individual while maximizing observations of independent events of species appearances (Yasuda, 2004). Photos were recorded at 3.0 megapixels, with a trigger speed of 0.6 seconds. Cameras used an infrared flash to capture photos in low-light.

Presence and individual detection rate (number of individual detections per day) recorded for each animal species. Human presence, activity, and number were also recorded. Data were extracted from the photos using the eMammal desktop application (eMammal, 2016).

2.4 Data Analysis

Descriptive analyses were performed in Microsoft Excel to determine the number of photos, sequences, effort, and species observed. Sampling effort was quantified as the number of camera trap days: number of camera traps deployed times the number of days deployed. The relative number of species detected was quantified by multiplying the number of species observed in each zone and phase by the effort in that zone and phase, then dividing by the average effort across all zone and phase combinations.

To answer our research questions, we analyzed two dependent variables: (1) occupancy probability and (2) detection rate for each of the treatment phases and both treatment zones. Occupancy probability measures the probability that a site (camera location in this case) is occupied by a given species. This analysis is based on binary detection/non-detection data, incorporates probabilities of false-negative detections, and accounts for imperfect detection through a hierarchical model framework (MacKenzie et al., 2006). Detection rate is a measure of the frequency each zone is visited by a species, based on rate of observation by the cameras. Five of the six target species were detected with sufficient frequency for occupancy analysis (squirrel, raccoon, coyote, turkey, opossum) and five species fit the detection rate regression models (deer, squirrel, raccoon, coyote, and turkey).

Deer occupancy was equal to 1 in several zone-phase data sets, making it impossible to answer our research questions using occupancy analysis due to lack of variation (Welsh, Lindenmayer, & Donnelly, 2013).

We performed a contrast, a method common in BACI studies, to answer the research questions regarding the effect of trail building and trail presence on terrestrial wildlife species in on-trail and near-trail zones. We tested for significance at the alpha level of 0.05. Contrast equations are shown in Table 3.1. For both types of analysis, a survey consisted of one camera trap day, with sampling occurring continuously throughout the 24-hour period starting and ending at midnight. To determine if sampling points were independent, we tested for spatial autocorrelation with Moran's I, using the 'ape' package in R (Paradis, Claude, & Strimmer, 2004). Using this test, a p-value greater than 0.05 indicates spatial clustering of the data.

Table 3.1. Contrast equations and corresponding treatment phases and zones. Model equations are provided with results from occupancy and detection rate analyses.

Zone and phase combination	**Contrast equation**
Near-trail during	Near-trail during – near-trail before – (control during – control before)
On-trail during	On-trail during – on-trail before – (control during – control before)
Near-trail after	Near-trail after – near-trail before – (control after – control before)
On-trail after	On-trail after – on-trail before – (control after – control before)

The effect of trail building and trail presence on the occupancy probability for each study species was determined using single-species, single-season occupancy analysis. For each sample point we created a detection history, a series of one's and zero's indicating detection and non-detection of the species for each survey, respectively (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). We ran Program MARK (White & Burnham, 1999) through the 'RMark' package in R (Laake, 2013) to model occupancy for the five species, with zone and phase as grouping variables and occupancy covariates, and detection distance and season as detection covariates (see Appendix A, Table A.1 for further explanation of model selection). For each study species, we assessed the significance of the zone*phase interaction term in the occupancy model to determine if the change in a species' occupancy probability between pre-building and treatment phases (during and after trail building) were significantly different in the treatment zones (on-trail and near-trail) as compared with the same period in the control zone.

The effect of trail building and trail presence on the detection rate for each study species was determined using a zero-inflated Poisson regression on the count of detections for each species per survey. Due to the dispersion and high proportion of zero values in our data, we determined that the zero-inflated Poisson regression would be an appropriate test for detection rate. We tested for goodness of fit using the Vuong test to determine which species fit the zero-inflated Poisson regression analysis (Vuong, 1989). This test showed that the zero-inflated Poisson regression model fit five of the six study species significantly better than did the ordinary Poisson regression model. We thus proceeded with analysis of these five species: deer, squirrel, raccoon, coyote, and turkey. We used the same covariates in this analysis as in the occupancy model (detection distance, season and a zone-phase term for both "count" and "zero" portions of the model). Analyses were conducted in R, using the 'pscl' package for zero-inflated Poisson regression (Jackman, 2015; Zeileis, Kleiber, & Jackman, 2008), and 'lsmeans' package (Lenth, 2015) to calculate least square means, combining "count" and "zero" model coefficients. Significance testing was performed using the contrast of least square means to answer our research questions regarding the effect of trail building and trail presence on the detection rate in on-trail and near-trail zones.

3. Results

We quantified the number of species observed, occupancy probability, and detection rate from 289,594 photographs containing 17 native mammal species and at least four bird species across all sites (Table 3.2). In total our data consisted of 7,386 unique photograph sequences capturing native mammals and birds at 301 sampling deployments (deployment refers to a camera set for a three-week period), with a total of 7,045 camera trap days of survey effort across all sites (Figure 3.2). Before trail building, 14 species were detected in both control and near-trail sites, while 12 were detected on-trail. During trail building, this number decreased to 11 in control and near-trail sites and increased to 13 on the trail. After trail building was complete, 12 species were detected in the control sites while both treatment sites had 11 species (Figure 3.3). Human use of the trail was exclusively diurnal, and was mostly construction workers and their vehicles during construction, and horseback recreation after construction (Figure 3.4).

Table 3.2. Full list of species observed in the study, and total observed for each species, in order from most to least number of detections.

Common Name	**Scientific Name**	**Camera Detections**
	Mammalian Species	
White-tailed Deer	*Odocoileus virginianus*	5872
Eastern Gray Squirrel	*Sciurus carolinensis*	1121
Northern Raccoon	*Procyon lotor*	755
Coyote	*Canis latrans*	260
Virginia Opossum	*Didelphis virginiana*	157
Unknown mouse or rat	*NA*	103
American Black Bear	*Ursus americanus*	81
Striped Skunk	*Mephitis mephitis*	74
Bobcat	*Lynx rufus*	48
Eastern Cottontail	*Sylvilagus floridanus*	30
Southern Flying Squirrel	*Glaucomys volans*	17
Gray fox	*Urocyon cinereoargenteus*	12
Red Fox	*Vulpes vulpes*	3
Eastern Spotted Skunk	*Spilogale putorius*	2
Woodchuck	*Marmota monax*	1
Long-tailed Weasel	*Mustela frenata*	1
Eastern Fox Squirrel	*Sciurus niger*	1
	Avian Species	
Wild Turkey	*Meleagris gallopavo*	192
American Crow	*Corvus brachyrhynchos*	30
Red-tailed Hawk	*Buteo jamaicensis*	3
Unidentified Owl	*NA*	3

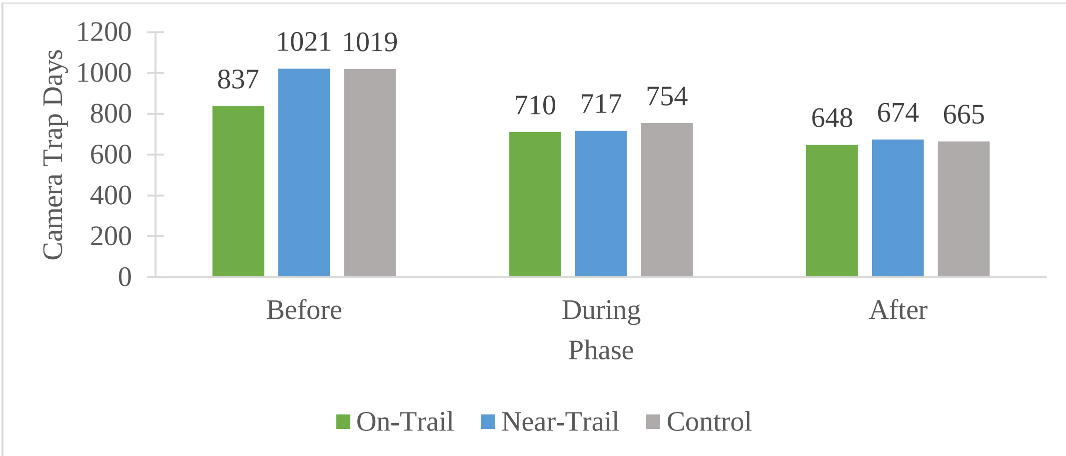

Figure 3.2. Effort for each zone during each phase of the project, measured in camera trap days.

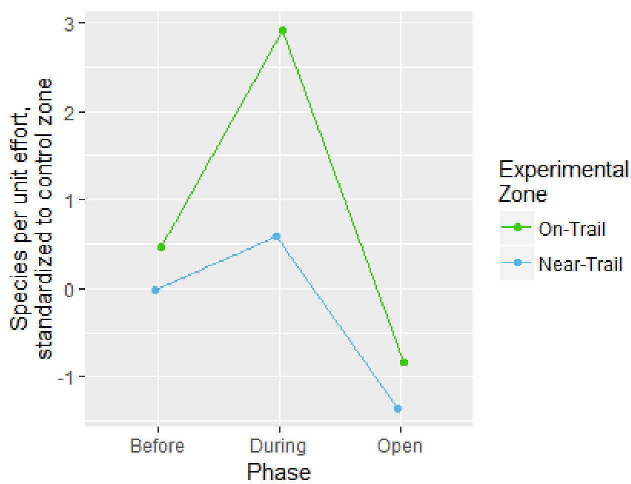

Figure 3.3. Difference between control and treatment sites in the number of species detected in each zone and phase.

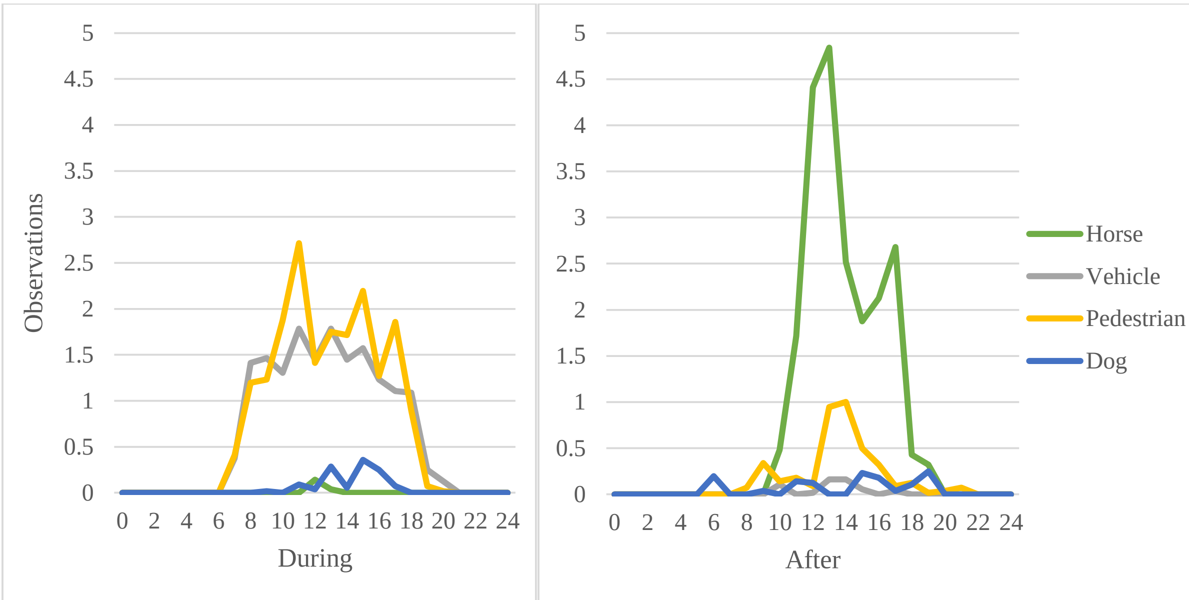

Figure 3.4. Hourly observations of human activity per hour during and after trail building, as a proportion of camera trap days. During trail building, nearly all pedestrian activity is the trail construction crew. Before trail building, only five recreationists were detected during the six month period.

3.1 Occupancy analysis

We conducted occupancy analyses for the five species with adequate detections for model convergence: squirrel, raccoon, coyote, turkey, and opossum. Three of these study species showed no spatial autocorrelation, while coyote and opossum had spatial autocorrelation (p=0.3025 and p=0.8461, respectively), indicating lack of independence between the sampling points. This could lead to an overestimated precision in occupancy estimates (Legendre, 1993), but is often not considered as accounting for spatial autocorrelation requires Bayesian analysis (Poley et al., 2014). For these five species, we analyzed the effect of trail building and trail presence in both on-trail and near-trail zones. Compared with the pre-building phase, the raccoon occupancy probability increased along the trail during trail building while it decreased in the control and near-trail zones (Figure 3.5b, Table 3.3). At the same time, coyote occupancy decreased in the near-trail zone while increasing in the control zone (Figure 3.5c, Table 3.3). Both of these discrepancies resulted in statistically significant differences in the change of occupancy probability before vs. during trail building. The data did not support other significant effects on the target species in trail building and trail presence in either treatment zone (Table 3.3).

Table 3.3. Occupancy probability (Psi) for each study species in each treatment phase and zone. Psi coefficients are those of the zone*phase occupancy probability interaction term for each contrast equation, with corresponding standard error and p-value. The occupancy model contains p~Detection Distance + Season; Psi~Zone*Phase; group = Zone, Phase. Each contrast is performed only on data for the specific zones and phases required. Cells with "NA" indicate that the model did not fit the dataset for the site and zone for the corresponding species. Highlighted cells indicate statistical significance of the contrast, at the alpha = 0.05 level.

	During, On-Trail			During, Near-Trail			After, On-Trail			After, Near-Trail		
Species	Psi	SE	p-value	Psi	SE	p-value	Psi	SE	p-value	Psi	SE	p-value
Squirrel	-0.41	0.78	0.61	-0.09	0.76	0.91	-0.34	0.93	0.73	-1.06	0.75	0.16
Raccoon	2.63	1.12	0.02	0.30	0.83	0.73	NA	NA	NA	NA	NA	NA
Coyote	-0.90	1.02	0.39	-2.48	0.97	0.01	0.56	1.09	0.62	-0.65	0.97	0.51
Turkey	-3.33	3.15	0.30	-1.41	3.11	0.66	NA	NA	NA	NA	NA	NA
Opossum	1.42	2.55	0.59	0.03	1.64	0.99	0.34	1.41	0.82	-0.15	1.17	0.91

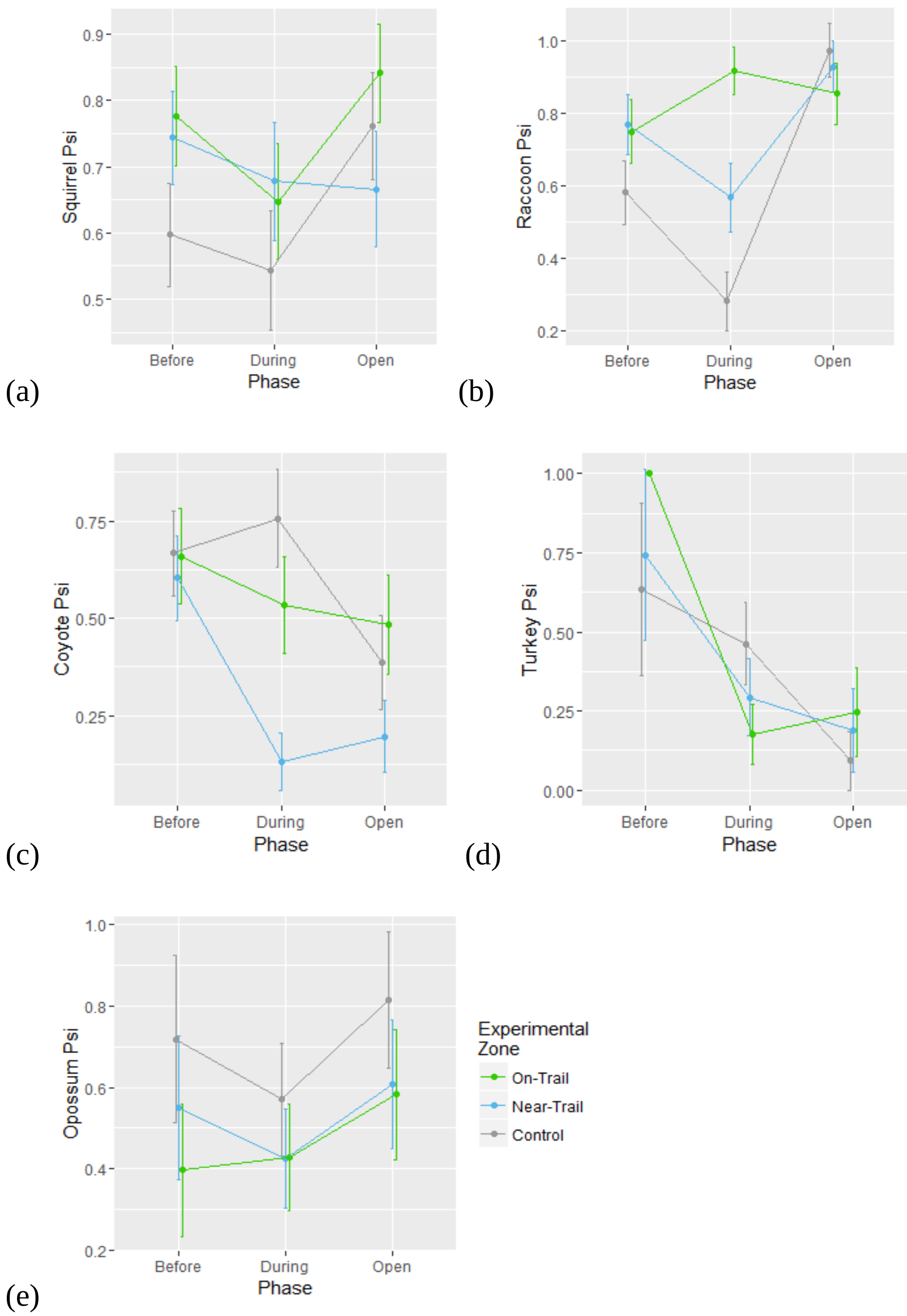

Figure 3.5. Occupancy probability (Psi) model estimates for each zone-phase combination for study species. Error bars show standard error. Points for which error bars do not overlap are statistically different, at the alpha=0.05 level. Significant relationships included: (b) Raccoon occupancy increased along the trail during trail building and (c) Coyote occupancy decreased near the trail during trail building.

3.2 Detection rate analysis

Five species had adequate detections for convergence with the zero-inflated Poisson regression model: deer, squirrel, raccoon, coyote, and turkey. We analyzed the effects of trail building and trail presence in both on-trail and near-trail zones using contrast equations on the least square means of detection rate resulting from these species' regression models. The data supported significant effects of trail building for raccoons and coyotes along the trail, and for deer and coyotes in the near-trail zone (Table 3.4). In the on-trail zone, raccoon detection rate increased during trail building while remaining relatively constant in the control zone (Figure 3.6c). Coyote detection rate decreased during trail building in both treatment zones while increasing in the control zone (Figure 3.6d). Deer detection rate also decreased during trail building in the near-trail zone while increasing in the control zone (Figure 3.6a). Squirrel detection rate decreased in the on-trail zone after trail building, while increasing in the control zone (Figure 3.6b). All other effects were not statistically significant (Table 3.4). These results were consistent with those obtained through occupancy analysis, and revealed more significant differences.

Table 3.4. Change in detection rate for the five study species during and after trail building in on-trail and near-trail zones, compared with the same change in the control zone, with model coefficient, standard error, and p-value. Detection rate equations included Zone-Phase + Detection Distance + Season covariates for both "count" and "zero" portions of the zero-inflated Poisson regression model. Highlighted cells indicate statistical significance of the contrast at the alpha = 0.05 level.

	During, On-Trail			During, Near-Trail			After, On-Trail			After, Near-Trail		
Species	Coeff.	SE	p.value	Coeff.	SE	p.value	Coeff.	SE	p.value	Coeff.	SE	p.value
Deer	-0.16	0.12	0.18	-0.41	0.12	0.00	0.15	0.08	0.07	0.05	0.08	0.53
Squirrel	-0.03	0.05	0.50	0.00	0.03	0.93	-0.20	0.04	0.00	-0.03	0.05	0.50
Raccoon	0.17	0.05	0.00	-0.01	0.03	0.62	0.00	0.03	0.89	-0.01	0.03	0.65
Coyote	-0.06	0.02	0.02	-0.07	0.02	0.00	0.00	0.02	0.98	-0.01	0.01	0.64
Turkey	-0.02	0.03	0.45	0.02	0.03	0.53	0.03	0.04	0.48	0.06	0.05	0.17

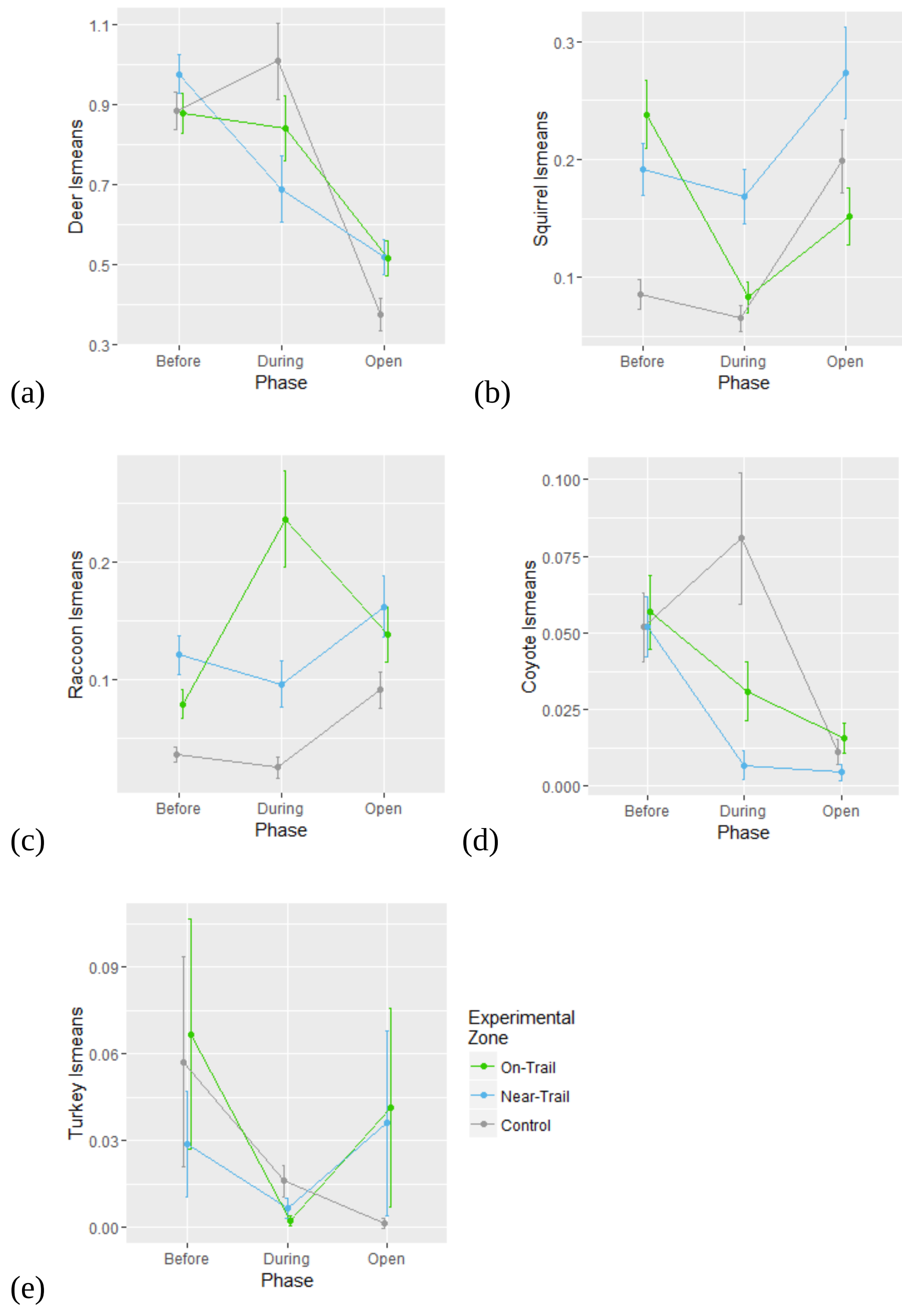

Figure 3.6. Detection rate for the experimental zones by five wildlife species across three seasons. Least square means (y-axis) is calculted from the least square means of the “count” and “zero” portions of the zero-inflated poisson regression model. Error bars which do not overlap are statistically different. Significant relationships included: (a) Deer detection rate decreased in the near-trail zone during trail building, (b) Squirrel detection rate decreased along the trail after trail building, (c) Raccoon detection rate increased along the trail during trail building, and (d) Coyote detection rate decreased along and near the trail during trail building.

4. Discussion

Our approach of using camera traps as part of a BACI experiment to evaluate the impacts of trail building and trail presence offers one of the strongest tests to date on this potential conflict between human recreational use and wildlife conservation. Overall, our results indicate that effects on wildlife are strongest during trail building, and arguably inconsequential once trail building is complete. We found that raccoons increased their use of the on-trail zone while coyotes slightly decreased use along and near the trail and deer substantially decreased use along the trail during trail building. Only one species, squirrel, showed significant effects of trail presence after construction, decreasing use along the trail, but had no significant difference in use of the near-trail zone. These results suggest that raccoons are attracted to the trail construction zone while deer and coyotes avoid the immediate area, with the zone of influence reaching at least 50m from the trail for deer and coyotes. Squirrels avoided the trail zone after building was complete.

Effects of trail presence on species occupancy paralleled the results of the detection rate analysis, but were less profound. Raccoons and coyotes had significant differences in occupancy during trail building compared with our control site and measurements of the same site before construction. These observations were consistent with changes in these species' detection rate, and suggest a pattern of displacement (coyote) and habitat expansion (raccoon) resulting from trail building. However, these effects were temporary, with occupancy returning to levels similar to the control zone after trail building was complete. If prolonged, this type of response could lead to human-shielded predator shelter or attractive sinks as found in previous studies (Hebblewhite & Merrill, 2007; Muhly et al., 2011; Roever et al., 2008; Shannon et al., 2014).

Raccoons were the only species to increase their use of either treatment zone during trail building, having increased use in the on-trail zone by 16.9%. Raccoons are known to be attracted to point sources of human disturbance such as garbage cans and often use edge habitat (Barding & Nelson, 2008). Nearly all trail building activity took place between the hours of 8am and 6pm, while raccoon activity peaks during nighttime hours. This temporal separation from human activity during trail building, combined with possible attraction to novel objects or food scraps left along the trail overnight likely explains why this species increased use along the trail during construction. Our results showed that raccoon use returned to levels similar to those observed in the control zone after trail building was completed. This observation indicates that raccoons do not disproportionately use trails, consistent with previous findings (Gompper et al., 2006; Miller & Hobbs, 2000).

Coyote detection rate decreased slightly both along the trail and in the near-trail zone during trail building (5.5% and 7.4%, respectively). These results suggest that coyotes avoided the on-trail and near-trail zones during high-intensity trail building activity. Coyotes have been observed to be leery of human presence and novel objects (Young, Mahe, & Breck, 2015), typical of the trail construction zone. White-tailed deer, a main source of food for coyotes in winter (Crimmins, Edwards, & Houben, 2012), also showed decreased use in the on-trail zone during trail building, which could have also resulted in less motivation for the coyotes to visit the study area during this project phase.

Squirrel was the only species that showed a significant effect from trail presence after construction, with detection rate decreasing by 20% on the trail once trail building was complete. We suggest that this decrease could be due to (1) avoidance of humans and/or (2) increased predation risk. In a previous study, squirrels with less exposure to humans had a larger flight initiation distance (Engelhardt & Weladji, 2011). In our study site squirrels had very low exposure to humans prior to trail building. Human recreational use of the trail occurred during daylight hours, overlapping with the period in which gray squirrels are active. Although recreational use was low, the decrease in squirrel trail use after trail building could be due to squirrels avoiding humans. Over time we predict that squirrels might habituate to humans along the trail. Decreased use of the trail zone by squirrels might also indicate avoidance of this open area due to the associated increased predation risk. During trail building, the trail zone had vegetation while it was in the process of being cleared. After construction was completed, this vegetation was entirely cleared from the trail, leaving fewer areas for squirrels to hide from predators. If human avoidance is the driving factor, squirrel use of the trail might increase over time as they become habituated to humans. However, if predation risk is more important, we expect that squirrels will be displaced from the trail zone in the long-term.

Our data did not support significant changes in other study species' use levels after trail building was complete. This is consistent with a recent study in an overlapping region, in which recreational trail use was not a consistently significant predictor of any of twelve species' use across all sites (Kays et al., *In Review*). However, this study found coyotes to use trails in 75% of study areas. Our results are not consistent with this finding, perhaps due to the comparatively smaller geographic scope or short period in which we collected data after trail construction was complete.

Deer was by far the most common species captured by cameras in this project. Deer occupancy was equal to 1 in several zone-phase data sets, making it impossible to answer our research questions using occupancy analysis due to lack of variation (Welsh et al., 2013). Our data showed that deer used the near-trail zone 41.3% less frequently during trail building, a period when near-trail human activity was somewhat frequent. This result is consistent with previous findings that near-trail activity resulted in greater impacts on deer than did on-trail activity (Miller, Knight, & Miller, 2001).

In previous studies, human approach on horseback was found to be less disturbing to deer than approach on foot (Kucera, 1976). Our result supporting a lack of change in detection rate of the on-trail zone once the trail was open for recreation is consistent with this finding, since most trail users were on horseback (Figure 3.4). However, human trail use during this study was low, and impacts of the trail are more likely related to the presence of the trail structure in the landscape leading to shifts in predator-prey relationships. Since deer resource selection is not believed to be highly influenced by predation risk (Kittle, Fryxell, Desy, & Hamr, 2008), the lack of change in deer trail use after the trail was completed is logical.

We found no significant changes in the occupancy or detection rate for wild turkey. This species is a habitat generalist and has been found to benefit from a heterogeneous landscape structure. Turkeys nest within forested habitats, raise their chicks in grassy habitats, use cornfields for food during harsh environmental conditions, and males use open habitats at forest edges to display (Rioux, Bélisle, & Giroux, 2009). Most previous studies have associated recreational activities with negative impacts on birds (Steven, Pickering, & Castley, 2011), including reduced intensity of habitat use for a species of grouse (Rösner, Mussard-Forster, Lorenc, & Müller, 2013). If similar effects are present in our study site, they were not detected using our methods.

Virginia opossum also did not show significant effects on occupancy related to trail building or trail presence. Previous research on opossums found no significant impacts of anthropogenic influences such as trail use in the Appalachian ecosystem (Erb et al., 2012), negative association with areas of bare earth, and positive association with percent of paved trail cover in an urban setting (Sinclair, Hess, Moorman, & Mason, 2005). The trail in our study is unpaved, and would be considered bare earth during and in the first few months after construction. We did not detect these possible changes in opossum detection rate, suggesting that if present, these effects are too small to be detectable using our methods.

5. Limitations

Several limitations of our study should be considered. We sampled twenty-one points per zone, repeated throughout the study period. This number of sampling points is recommended by some wildlife researchers (Kays et al., 2011; Si, Kays, & Ding, 2014) but is fewer than the number recommended by others (Rovero et al., 2013). As this is a relatively small study zone, we defend the use of this number of sampling points as representative of the study area.

Another limitation is the lack of on-trail points throughout the project. Although there are abandoned human trails (old logging roads) present in both treatment and control zones, only two of the sampling points were randomly assigned to locations along these existing pathways. This restricts our analysis of the effect of trail presence to a before/after analysis, whereas we might have been able to analyze the impact of human trail presence on species throughout the entire year had more sampling points been placed along the existing trail.

Although we detected a total of seventeen mammalian species and more than four bird species, our analysis was limited to the six most common species in the study area, which were detected with enough frequency to fit the occupancy and/or regression analyses. Species detected less frequently might show responses to trail building and/or trail presence not detected here. Future analysis using different methods might reveal responses of more species to trail building and presence.

The study area is not pristine. Existing recreational trails lie within 275m of both study zones, and other park infrastructure such as roads lie within 460m. Recreational activity was present along a logging road in the treatment area until 2008. Species with larger home ranges or with a life span greater than 7 years may thus have already been habituated to human use. The results presented here are restricted to the study site and year. Additionally, the study trail had a low level of human use once it was opened to recreationists, with an average of 1.42 people per day. However, since most protected areas in which trails are built have nearby human activity, we believe that our study area is appropriate for the research questions and results can inform future research and management.

Considering these limitations, we argue that our results are strong and indicative of the impacts of trail building on the temperate wildlife community. As the first study investigating the effects of trail building on wildlife activity using an experimental design, these results will serve as a foundation for future studies expanding on this work.

6. Management Implications and Conclusions

Impacts on the target species were almost entirely restricted to the trail building phase in this study. The data supported significant impacts of trail presence only for the eastern gray squirrel, which decreased their use once the trail was opened to recreation, but this effect did not extend into the near-trail zone. We conclude that most effects of the creation of the trail were restricted to the trail construction itself. However, the lack of impacts detected after trail building was complete is also likely influenced by the low level recreational use of the trail. Future work investigating similar impacts on a higher use trail are recommended to further explore the effects of trail use on wildlife.

Trail construction affected four species in the on-trail zone, and two of these species showed responses up to at least 50m from the trail. Although all of the species studied here were common in the study area, the fact that four of the six species studied were affected suggests that other species around the world might also be affected by trail construction activities. In areas where endangered species are present, impacts could be reduced if managers (1) restrict construction to a short time period and (2) consider the life cycle of endangered species potentially affected by trail construction when determining the season in which construction will occur. Taking an example of one of our study species, coyotes den during the spring and are known to move den sites following human disturbance (Harrison & Gilbert, 1985). Trail building during the denning season could thus imply additional energy requirements from adults and make coyote pups more vulnerable to predation if den sites are moved. If the local coyote population declines, prey species such as white-tailed deer, could increase in abundance (Gulsby et al., 2015). If impacts such as those observed in this study persist, the predator-prey balance may shift in the local area, likely having cascading effects on the surrounding ecosystem. Furthermore, if endangered species are displaced during trail building, poorly timed construction might further threaten the species' local population.

The trail constructed during this project used a motorized approach, with equipment such as excavators, all-terrain vehicles, chain saws, leaf blowers, and motorized trail compactors. In our study, an average of sixteen passes by motorized vehicle and nineteen passes by trail crew members on foot occurred along the trail per day during construction. Future research regarding the difference between impacts of mechanized and manual trail construction would be an interesting contribution to management in designated Wilderness areas, where the use of motorized equipment is highly restricted. Previous research found that non-motorized recreation resulted in greater impacts to several wildlife species than did motorized recreation (Harris, Nielson, & Rinaldi, 2014; Kucera, 1976). However, a review found motorized recreation to displace a larger number of species over longer distances than did non-motorized recreation (Gaines, Singleton, & Ross, 2002).

Our findings indicate short-term habitat reduction and expansion for two species during trail building, attraction and avoidance for three species during trail building, and avoidance for one species after the trail is open. To draw conclusions regarding habituation of species to the trail, long-term monitoring data must be collected. Further research might reveal if trail presence affects the species studied here in the long term, such as large predator species using the trail for movement during periods of low human trail-based activity, as seen in previous studies (Cusack et al., 2015; Harmsen et al., 2010; Karanth & Nichols, 1998), or a shift in predator-prey balance as previously mentioned.

Wildlife preservation is an important part of protected area goals to conserve natural ecosystems and provide quality nature-based recreation opportunities. The research presented here, in combination with many previous studies investigating interactions of humans and wildlife in a rural setting, can inform science-based protected area management to minimize the negative impacts of recreation, improving the provision of recreational resources on the natural areas in which they occur. In our analysis we found that long-term impacts of a new trail, if any, are likely restricted to the immediate trail zone and limited to one common species. Our study thus demonstrates that recreation and wildlife can coexist and need not be exclusive.

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CHAPTER 4. Recreational Trail Construction Alters Community Composition for Terrestrial Vertebrates: An Appalachian Case Study

Abstract

Protected areas often have the dual goals of conserving biodiversity and providing recreation opportunities to the public. However, these goals can conflict if recreation, wildlife, or habitat are not managed effectively. Recreational trails are linear structures common to protected areas which have a range of potential impacts on the surrounding ecosystem. Previous research has shown that species richness often decreases due to anthropogenic disturbances associated with recreation on trails. Such disturbances also shift predator-prey relationships in many protected areas. In this study we implement a before-after control-impact (BACI) experimental design using camera traps to investigate the impacts of trail construction on wildlife community composition. We analyzed 8,730 detections of eighteen terrestrial vertebrate species made from camera trap images, to assess the change in species richness across phases of trail construction and between treatment and control zones. We found that larger predators (coyotes and bobcats, *Canis latrans* and *Lynx rufus*) had decreased detection rates during and after trail building while a smaller predator (gray fox, *Urocyon cinereoargenteus*) had increased detection rates in the on-trail and near-trail zones during this time, suggesting a mesopredator release effect. Increased species richness in the on-trail and near-trail zones during trail building was driven by rare species and corresponded with decreased detection rates of the most common species. This result

suggests that rare species become relatively more active and common species become less active in periods of intense human activity such as trail construction. This finding also concurs with the human shield hypothesis, suggesting that smaller predators and prey species use human presence on and near the trail as a potential refuge from predation risk. After trail building was complete, species richness returned to nearly pre-trail levels along the trail and decreased slightly in the near-trail zone. Trail building could temporarily benefit prey species, an implication which is particularly important where endangered prey species are present. However, this effect might revert as predators become habituated to the trail and the human activity it brings.

Keywords: wildlife, trail, recreation, before-after control-impact, experiment, camera trap, species richness

1. Introduction

Recreational trails are linear structures found even in strictly protected areas (Dudley, 2008) which have a range of potential impacts on the surrounding ecosystem. Trails create edge habitat, lead to the spread of invasive plant species, change hydrological patterns, alter the composition and structure of soil and vegetation communities, and lead to habitat fragmentation (Ballantyne et al., 2014; Ballantyne & Pickering, 2015; Leung, 2012; Sutherland et al., 2001; Wimpey & Marion, 2011). This shift in physical, vegetative, and microfauna community structures contributes towards habitat alteration and might be exhibited in the terrestrial vertebrate community on a local scale.

Species richness, the number of species present in an assemblage, is a widely used indicator of biodiversity and community structure by community ecologists and conservation biologists (Gotelli & Colwell, 2011; Hubbard, 2013). Recreational trails are associated with reduced native species richness in several taxonomic communities, including plant communities (Ballantyne & Pickering, 2015), soil- and litter-dwelling invertebrates (Littlemore & Barlow, 2005), birds (Miller, Wiens, Hobbs, & Theobald, 2003; Wolf, Hagenloh, & Croft, 2013), and both terrestrial and arboreal mammals (Cunha, 2010; Reed & Merenlender, 2011).

Although species richness is a useful indicator of changes in community structure, this metric does not reveal where such changes lie. In fact, species richness can remain constant while the species present in an area change substantially (Gotelli & Chao, 2013). For example, recreational activity can alter bird community composition, with species present shifting, while richness remains constant (Kangas, Luoto, Ihantola, Tomppo, & Siikamäki, 2010). To detect shifts in community composition, it is necessary to look further into the activity level of the species present, specifically considering the niche each species fills within the ecosystem.

Anthropogenic disturbances are associated with shifted predator-prey relationships in many protected areas. The human shield hypothesis suggests that shifts in predator-prey relationships can be caused by prey species using human use areas as shelter from potential predators (Berger, 2007; Muhly et al., 2011; Shannon et al., 2014). This phenomenon was observed in a study investigating the impacts of a new paved path on wildlife in Grand Teton National Park. This before-after control-impact (BACI) study found avian and mammalian prey species to use areas directly surrounding a new trail as refuge from predators (Brown et al., 2012; Chalfoun, 2011, Shannon et al., 2014). Building upon this interaction, the mesopredator release hypothesis suggests that in the absence of large predators, mesopredators (middle trophic level species which both prey and are preyed upon) increase in abundance due to release from predation and competition (Crooks & Soulé, 1999; Prugh et al., 2009). Support for this hypothesis has been widely documented in a variety of ecosystems globally and is associated with human use areas. An example relevant to our study is the reduction of bobcat and coyote abundance corresponding with an increase in fox abundance (Cove et al., 2012; Ordeñana et al., 2010). Considering activity level for different trophic groups in combination with species richness improves researchers' ability to determine if human activity associated with recreation alters local ecosystem dynamics.

The literature on human-wildlife interaction is extensive. However, most research in this area is based on correlation and lacks elements of the BACI experimental design. In our literature review, we found no previous studies investigating the impacts of trail building on the terrestrial vertebrate community composition. Additionally, most literature investigating anthropogenic impacts on species richness has focused on plants, birds, and invertebrates, with far fewer published studies investigating mammalian species richness. With the large increase in the use of camera traps in recent years, mammalian species richness has become easier to quantify. Using camera trap data within a BACI design, both species richness and detection rate can help us understand the impacts of trail building, a wide-spread visitor use management activity occurring throughout the world, on the terrestrial vertebrate community.

In this study we investigated the impacts of new trail construction on community composition, using an equestrian trail built in the southern Appalachian Mountains as a case study. Through a BACI experimental design, we were able to isolate the change in species richness and detection rates of different trophic groups in the terrestrial vertebrate community due to the treatments of trail building and trail presence. We addressed the research question: How does trail building affect species richness and detection rates for the terrestrial vertebrate community on and near the trail? We believe that this study is the first of its kind, as the few previous BACI studies on recreational trails do not include the construction phase.

2. Methods

2.1 Study Site and Data Collection

We collected data in a year-long study at Stone Mountain State Park, North Carolina, from August 30, 2014 through September 12, 2015. This 57-km^2 park is in a rural area and contained occupied homesteads until the late 1960s, when it was designated as a state park. Several abandoned logging roads run through the site, one of which was used as an equestrian trail until 2008. The site also has other recreational areas within 275m and roads within 460m. We used the number of individual detections by each camera trap per day as the number of detections for each animal species. See Chapter 3 of this dissertation for further detail regarding the study site and data collection methods.

In this study we used data from three sites (control, on-trail, and near-trail zones) and three phases (before, during, and after trail building). We discuss analysis and results in terms of treatment zones (on-trail and near-trail) and treatment phases (during and after trail building), using data collected in the control zone and in all zones prior to trail building as baseline data. Each camera trap day was treated as one survey period.

2.2 Data analysis

We used three methods to answer the research question regarding the impact of trail building and trail presence on terrestrial wildlife species richness and community composition. First, we plotted the species accumulation by sample, in our case one survey period (camera trap day), using rarefaction (EstimateS 9.1.0, Colwell, Mao, & Chang, 2004;

Colwell, 2013) for each of the nine zone and phase combinations throughout the project (i.e. before/control, during/control, after/control; before/on-trail, during/on-trail, after/on-trail; before/near-trail, during/near-trail, after/near-trail). Rarefaction is a method which uses random re-sampling from a pool of samples, in our case 100 times, then plots the average number of species found in each sample. These curves generally grow quickly at first, as the most common species are found, and slow when enough samples have been made to approach an asymptote, at which only the rarest species remain to be sampled. From these curves we determined whether datasets from each zone and phase of the project had reached an asymptote, which would indicate that the samples were complete. In the case that an asymptote is not reached, species richness estimators are often used to extrapolate species richness to the presumed asymptote, beyond which additional sampling will not yield new species (Gotelli & Chao, 2013). Since nearly all curves did not reach an asymptote (see Appendix B, Figure B.1, for rarefaction plots), we expected that the actual species richness exceeded the observed species richness. To reduce underestimation of species richness, we continued our analysis using a species richness estimator, as described below.

We chose to use the Chao1 species richness estimator to represent our sample, due to its sensitivity to rare species (Magurran, 2004). This non-parametric estimator is based on the concept that rare species carry the most information about the number of undetected species and estimates species richness using only the numbers of species observed once (f_1) or twice (f_2) in a dataset to obtain the lower bound for the expected asymptotic species richness, as calculated by the following equation:

$$\hat{S}_{Choa1} = \begin{cases} S_{obs} + \dfrac{f_1^2}{2f_2} & if\ f_2 > 0 \\ S_{obs} + f_1(f_1 - 1)/2 & if\ f_2 = 0 \end{cases}$$

with an associated variance estimator of (if $f_2 > 0$):

$$v\hat{a}r(\hat{S}_{\text{Chao1}}) = f_2 \left[\frac{1}{2} \left(\frac{f_1}{f_2} \right)^2 + \left(\frac{f_1}{f_2} \right)^3 + \frac{1}{4} \left(\frac{f_1}{f_2} \right)^4 \right]$$

where S_{obs} is the observed species richness and $\hat{S}_{Chao1}$ is the estimated species richness (Chao, 1984; Gotelli & Chao, 2013). Having separated our data into nine zone/phase data subsets, several species had only one or two observations in a data subset although they might be common in the area. We were interested in retaining these species in our analysis, as we expect that these species are sensitive to trail building. We thus chose the Chao1 species richness estimator as we expected it to best represent the number of species in each zone and phase under these conditions.

We did not expect immigration or emigration of species from the study site or control site within a phase of our study, with each phase lasting three to six months. Considering this, we treated species richness as a measure of the number of species present and active in the assemblage (henceforth referred to as active species richness). Using the Chao1 estimates of active species richness for each zone and phase, we subtracted the estimate for the control site from both treatment sites to remove variation unrelated to the treatment. We plotted these differences to demonstrate the relative change in active species richness between phases in both treatment zones (on-trail and near-trail). Species richness was calculated with EstimateS

9.1.0 with 100 runs and randomization without replacement. We used a cutoff of 679 camera trap days, the size of the smallest dataset.

We next investigated the change in active species richness between the baseline data and treatment phases (during and after trail building) for the treatment zones. Using a two-sample t-test, we compared the mean species richness change between the before phase and each treatment phase in the two treatment zones with the corresponding change in the control zone. We then performed a contrast, a method common in analyzing data for the BACI design (McDonald, Erickson, & McDonald, 2000), to find the magnitude of the difference in the changes between phases in the treatment zones and the control zone. Contrast formulas are shown in Table 4.2.

To assess community composition, we calculated the detection rate for each species, corrected for effort by dividing the number of detections by the effort in camera trap days for the corresponding zone and phase. Five species (woodchuck, eastern fox squirrel, long-tailed weasel, spotted skunk, and red fox) were detected one to three times throughout the project, and were thus considered cryptic or transient and disregarded from analysis of detection rate, though they are known to be present in the area. We determined the primary trophic category (herbivore, omnivore, or carnivore) and predator group from information provided in an online database (Myers et al., 2014). Using these detection rates we calculated the same contrasts as were calculated for estimated species richness to determine whether each species' detection rate increased, decreased, or remained constant during the treatment phases in treatment zones relative to the control zone (see Appendix B, Table B.2 for detection rates). To graphically compare trends between species, we took the natural logarithm of the detection rate contrast for each species (Figure 4.4). We identified patterns in detection rates for each trophic category, focusing on the relationship between large predators, mesopredators, and prey species.

3. Results

We quantified species richness and detection rate from 8,730 detections of seventeen native mammal species and one large terrestrial bird (see Table 3.2 in the previous chapter for a full species list, see Table B.1 in Appendix B for standardized number of detections per species per zone and phase). We collected data for a 54-week period, resulting in a total of 7,045 camera trap days of survey effort across all sites (see Figure 3.2 in the previous chapter for the breakdown of effort per site and phase). Results for contrast analyses of species richness and detection rates are discussed in terms of increase and decrease in the amount of change for both estimated species richness and detection rate between phases, compared with the control zone.

3.1 Species richness

We found different patterns of species accumulation between zones for each phase, using the Chao1 species richness estimator (Figure 4.1, Table 4.1). After subtracting estimates in the control site from both treatment sites, we found that estimated active species richness, or the number of species present and active in a zone and phase, was higher in both on-trail and near-trail zones during trail building, and slightly increased (on-trail) or decreased (near-trail) once the trail was complete, compared with pre-building levels (Figure 4.2). This pattern was more pronounced in the on-trail zone, with active species richness peaking at 4.63 and 1.73 more species active in the on-trail and near-trail zones than in the control zone, respectively. Species which appeared in the on-trail zone during trail building which were not previously present in this zone included gray fox, eastern spotted skunk, and woodchuck. In the near-trail zone during trail building, eastern spotted skunk appeared though not previously observed in this zone. After trail building, gray fox appeared in the on-trail zone and long-tailed weasel appeared in the near-trail zone, while these species were not observed in these zones before trail building. Further variation in the estimated species richness between zones likely results from variations in the frequency of observation of other species or latency to observation of rare species, as the estimated richness value is calculated as an average of randomized samples from the dataset.

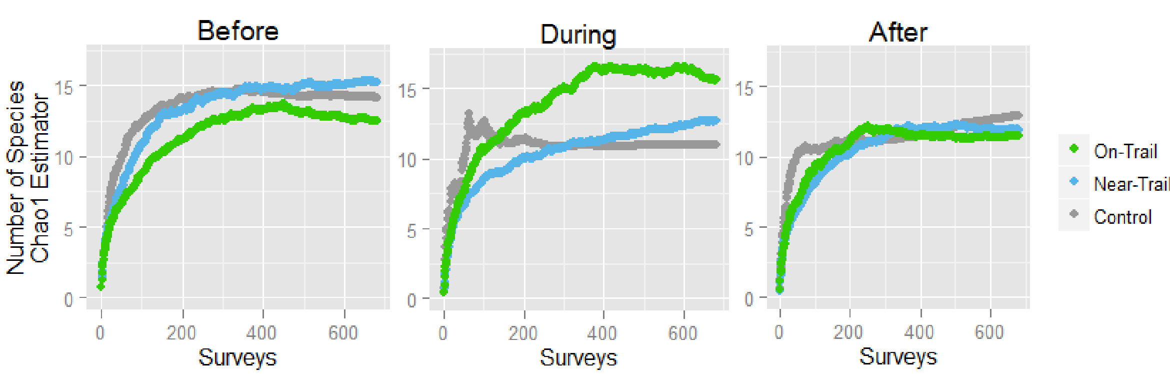

Figure 4.1. Species accumulation estimated with the Chao1 non-parametric species richness estimator by survey for each zone and phase. Plotted values for Chao1 are means of 100 randomizations of survey order, without replacement. Since the Chao1 species richness estimator is simulated and based on species with one or two observations, the estimated species richness does not always follow a single direction of accumulation. Each survey is one camera trap day.

Table 4.1. Number of active species in each zone and phase, with standard deviation, based on the Chao1 species richness estimator. Values provided are for 679 surveys.

	Before		During		After	
Zone	Mean Active Species Richness	Standard Deviation	Mean Active Species Richness	Standard Deviation	Mean Active Species Richness	Standard Deviation
On-Trail	12.48	1.61	15.63	4.34	11.50	1.32
Near-Trail	15.21	3.45	12.73	3.47	11.95	2.31
Control	14.16	0.96	11.00	0.05	12.90	2.21

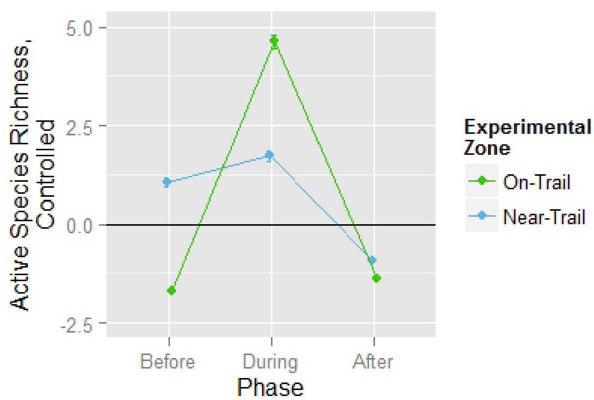

Figure 4.2. Difference between the number of active species in on-trail and near-trail zones and the control zone, for all three project phases. Active species richness is estimated using the Chao1 estimator and 679 surveys. Subtracting the richness in the control zone from the treatment zones removes unrelated effects on species richness such as seasonality.

We used contrast equations to compare the change in active species richness between treatment phases for treatment zones with the change in the control zone for the same period, as shown in Table 4.2 and Figure 4.3. We also used two-sample t-tests to analyze phase changes, supporting significant differences in the change of active species richness between the "before" phase and both treatment phases for on-trail and near-trail sites, compared with the corresponding change in the control site ($p<0.001$ for all four tests) (Table 4.2). Thus, our data suggests there was a significant impact of the trail on the number of active native terrestrial species both along the trail and in the 25-50m corridor surrounding the trail, during and after trail building. During trail building, near-trail active species richness increased by 0.68 species more than the control site did during the same period, while on-trail active species richness increased by 6.31 species more than the control site. After trail building was complete, the near-trail active species richness decreased by 2.00 species more than the control site, while the on-trail zone increased by an estimated 0.28 species more than the control site during the same period.

Table 4.2. Contrast equations and corresponding differences in Chao1 species richness estimators at 679 surveys. Pooled standard deviation, computed t-statistic, and probability of computed t are from the t-test comparing the change in estimated species richness in the treatment zone with the corresponding change in the control zone, as indicated in the contrast equation.

Contrast Equation	**Difference in Chao1**	**Pooled Standard Deviation**	**Computed t Statistic**	**Probability of computed t**
Near-trail During – Near-trail Before – (Control During – Control Before)	0.68	0.007	92.590	p<0.001
On-trail During – On-trail Before – (Control During – Control Before)	6.31	0.007	906.239	p<0.001
Near-trail After – Near-trail Before – (Control After – Control Before)	-2.00	0.007	-282.890	p<0.001
On-trail After – On-trail Before – (Control After – Control Before)	0.28	0.005	59.704	p<0.001

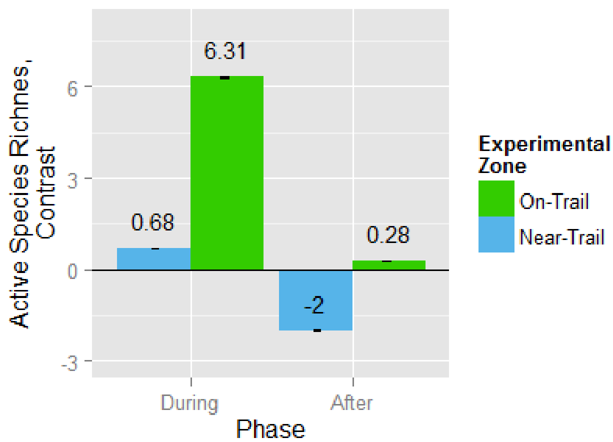

Figure 4.3. Difference between treatment and control zones in the change of the number of active species between each treatment phase ("during" and "after") and the "before" phase. Active species richness is estimated using the Chao1 species richness estimator. Full contrast equations are shown in Table 4.2.

3.2 Community composition

The most prominent pattern in the response of different trophic groups to trail building, based on the contrasts performed with detection rates for each species was found in the carnivorous species, bobcat, coyote, and gray fox (Figure 4.4). Carnivores showed two distinct patterns: two large carnivores had decreased detection rates in all four treatment zones and phases (coyote, bobcat) while smaller carnivores had increased detection rates in all four treatment zones and phases (gray fox).

Overall, in the on-trail zone after trail building was completed, eight species had a reduced detection rate and five had increased detection. Nearly all species whose detection rate increased on-trail after trail building also increased in the near-trail zone during this period, and vice versa (most species which decreased on-trail also decreased in the near-trail zone). Such a distinct pattern was not observed in the two treatment zones during trail building.

Finally, the eleven most common species (those with at least thirty observations in the entire study) mostly decreased in treatment zones while the two less common species (those with between four and thirty observations) increased during and after trail building in the treatment zones (Figure 4.4). Five species were detected less than four times during the project, and were omitted from the analysis of detection rate. However, it is worth noting that three of these species were observed only during treatment phases in the treatment zones. Woodchuck appeared in the on-trail zone during trail building, spotted skunk appeared twice during trail building (once on-trail and once near-trail), and long-tailed weasel appeared in the near-trail zone after trail building. Red fox and eastern fox squirrel appeared only before trail building and were not observed again during the project.

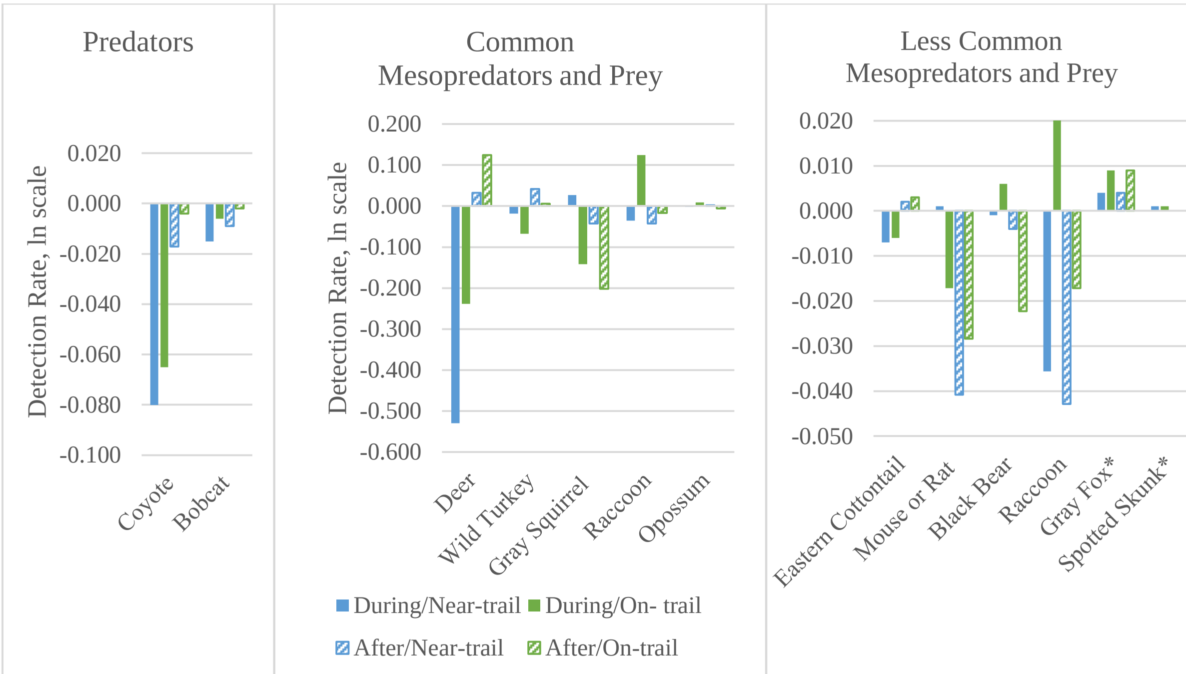

Figure 4.4. Detection rate contrast for each species, calculated according to the equations shown in Table 4.2. Detection rates are shown on the natural log scale. Species with an asterisk (*) are considered rare in the dataset, with fewer than thirty observations.

4. Discussion

As we did not expect immigration or emigration of species from the site within the three- to six-month phases of this year-long study, we considered the estimated species richness to represent the assemblage of species present and active during each phase and zone of this study, referred to as "active species richness" (see Methods). According to this interpretation, an increase in estimated species richness indicates increased activity from a wider range of species as compared with the control zone and pre-treatment phase. We will discuss our results according to this interpretation for overall species richness and detection rate for groups of species.

4.1 Species richness

Our findings suggest that new recreational trail construction and presence impact the terrestrial vertebrate community activity in our Appalachian study site. Statistically significant changes in active species richness were found in both treatment zones during both treatment phases, when compared with the control site. After the trail was complete, the number of active species increased slightly by 0.28 species in the on-trail zone and decreased substantially by 2.00 species in the near-trail zone. Although statistically significant, we do not consider the increase in 0.28 active species in the on-trail zone ecologically significant. Considering that the largest estimated active species richness of any data subset was 15.63, a decrease in 2 species could have important implications on community structure. Previous studies have found reduced mammalian species richness associated with recreational trails (Cunha, 2010; Reed & Merenlender, 2011). A recent meta-analysis of declines in local species richness found that human disturbance from land-use change, invasive species, and habitat loss to reduce species richness across all taxa by 24.8%, 23.7%, and 14%, respectively (Murphy & Romanuk, 2013).

During trail building, the number of active species increased by 6.31 species on-trail and 0.68 species in the near-trail zone. However, most published literature associates human activity with reduced mammalian species richness (e.g. Reed & Merenlender, 2011). Our finding of increased active species richness along the trail during construction corresponds with increased detection rate of rare species during this phase. Nearly all species with fewer than 30 detections during the project (i.e. red fox, gray fox, southern flying squirrel, eastern spotted skunk, and long-tailed weasel) had increased detection rates during and after trail construction in the treatment site. Meanwhile, the most common species often showed decreased detection rates in these phases and zones as compared with pre-trail and control zone data. This suggests that intense human disturbance, such as trail building, could result in increased activity level of rare species in the short term. Increased mammalian species richness associated with human disturbance is a new finding in this body of literature and could have important implications in areas where endangered species are rare.

4.2 Community structure: Predator-prey dynamics

Our results regarding the relative detection rates of tropic groups are consistent with the human shield hypothesis (Berger, 2007; Muhly et al., 2011; Shannon et al., 2014). In our study, several prey species (e.g. gray fox, southern flying squirrel, white-tailed deer, raccoon, and eastern cottontail) had increased detection rates associated with trail building and/or presence, while both large predators (bobcats and coyotes) decreased. Prey species may be occupying this human use zone as a shelter from potential predators. Our results also support the mesopredator release hypothesis. While both large predators, bobcats and coyotes, had decreased detection rates in all treatment zones and phases, one mesopredator (gray fox) had increased detection rates associated with trail building and trail presence. Previous studies have found mesopredators such as foxes to have greater abundance where the abundance of larger predators, such as bobcats and coyotes, is lower (Crooks & Soulé, 1999; Ordeñana et al., 2010). Additionally, coyotes are known to kill sympatric fox species (Lesmeister, Nielsen, Schauber, & Hellgren, 2015), and red foxes have been found to use human-altered habitats, such as trails with high human use, generally avoided by coyotes (Erb et al., 2012; Gosselink, Deelen, Warner, & Joselyn, 2003). Other mesopredators in our study, raccoons and striped skunk, decreased in several treatment zones and phases, consistent with other studies finding these species to be unaffected by other carnivores (Gehrt & Prange, 2006; Lesmeister et al., 2015; Ordeñana et al., 2010). Our results showing decreased activity in both treatment zones for coyotes and bobcats and simultaneous increased activity for gray foxes supports the mesopredator release hypothesis and is consistent with previous findings for these species.

Our results are also consistent with previous findings on the activity of bobcats, coyotes, and mule deer in a recreation area in California (George & Crooks, 2006). In this study bobcats and coyotes exhibited spatial and temporal displacement in response to human recreation, while mule deer did not exhibit consistent displacement related to recreation activity. Similarly, in our study bobcats and coyotes had decreased activity while white-tailed deer had increased activity associated with human activity.

A recent study in an overlapping area found that coyotes, and to a lesser extent bobcats and foxes, often preferred human trails to other habitat (Kays et al., *In Review*). Other studies have also found that large predators, such as coyotes and large cats, prefer trails (Cusack et al., 2015; Harmsen, Foster, Silver, Ostro, & Doncaster, 2010; Karanth & Nichols, 1998; Kays et al., 2011). We did not find this result in our data, as coyotes and bobcats had reduced detection rates in the on-trail and near-trail areas both during and after trail building.

As the trail in our study was either under construction or in the first few months of completion, this result could indicate that coyotes are leery of intense human activity such as trail construction. Future studies should further investigate this discrepancy to determine if there is lag time between a period of intense human activity in which large predators such as coyotes and bobcats have reduced detection rates before returning to the area, perhaps in higher intensity due to their preference for the trail. If true, this lag time would be the period observed in this study, in which foxes fill the predator niche in the relative absence of larger predators.

From these results we can hypothesize the occurrence of a complex predator-prey interaction. First, human activity during trail building creates a predator shelter zone, pushing out large predators and allowing prey to move into these areas. The relative decrease in predator presence then results in the release of mesopredators, who feed on smaller prey species, resulting in cascading effects through the food web. Understanding which factors drive the relative decrease in predator detection rates and increase in mesopredator/prey species detection rates will help us predict and manage long-term effects of trail building. For example, if this effect is driven by the human shield created during trail building, we would expect that this effect would dissipate if human trail use continues to be light, or continue if human trail use increases in the future. However, if the effect is driven by the release of mesopredators, we would expect these mesopredators to maintain high detection rates regardless of human activity level, as long as large predators do not return to the area. Effective management strategies differ for these two scenarios. In the human shield-driven scenario, the intensity of human use along the trail would likely have substantial influence on predator-prey relationships. However, if mesopredator release drives the shift, large predators would need to return to the area and become habituated to human trail activity to restore pre-building levels of prey species.

5. Conclusions

This study demonstrated that the number of species present increased during trail building and decreased after trail construction was complete. Our findings support the human shield hypothesis, with several prey species having increased detection rates around the trail during and after building. Our data are also consistent with the mesopredator release hypothesis, with the increased detection rate of mesopredator species coinciding with decreased detection rates of larger predators. Species richness patterns and detection rate shifts generally extended from the on-trail zone into the near-trail zone, indicating that the effect of trail construction and presence exist along a corridor of at least 100m through the study area, although with a stronger effect along the trail itself.

Our implementation of the BACI experimental design provides the capacity of drawing causal inference, absent from many previous observational studies which based conclusions on correlations. Many of our results for trophic groups and individual species are consistent with previous findings from a wide range of forested ecosystems across North America (e.g. Brown et al., 2012; Erb et al., 2012; George & Crooks, 2006; Kaminski et al., 2007; Lesmeister et al., 2015). We thus believe our results to be applicable in temperate forest ecosystems such as those in North America.

Our findings suggest that common species become less active and rare species become more active during trail building. This could be due to several factors, including an increased availability of resources previously used by common species, habitat becoming more suitable to previously rare species, or decreased predation risk as discussed above. This effect might also change as common species become habituated to the trail and the human activity it brings. A recent meta-analysis showed that mammals, birds, and lizards in disturbed areas are more tolerant of human disturbance than those in less disturbed populations (Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015). With the increased disturbance introduced through the new trail, we expect that species will become more tolerant to human activity in the future. In our study, human use of the trail was very low in the first three months after it was open, with an average of 1.42 people per day. Future studies should investigate the long-term effects of trail building on the terrestrial wildlife community and expand this work to areas with higher intensity human use. Results from such studies could better inform management practices to minimize environmental impacts of human recreation.

Our analysis did not return obvious patterns in relative detection rates regarding temporal activity patterns (i.e. nocturnal vs. diurnal species). However, it is likely that the activity of nocturnal species is less affected than diurnal species, since trail building and recreation typically occur during daylight hours. Further research should investigate the impact of trail building daily activity patterns using a fine-scale approach to correspond levels of human activity with wildlife activity patterns. This analysis would be particularly important in areas where endangered species are present, improving management of these species. Finally, future work extending results from this and similar studies beyond the first few months after trail completion will improve our understanding of the long-term effects of trail building on terrestrial wildlife community composition.

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CHAPTER 5. General Conclusions

Introduction

The goal of this dissertation was to investigate the impact of recreational trails on the terrestrial wildlife community. To do so, we first developed a method to simultaneously quantify human and wildlife activity along a trail, asking the research question, "How effectively can human trail-based activity be quantified using a camera trap method consistent with methods developed to capture terrestrial wildlife?" We then implemented this method in a before-after control-impact (BACI) experimental project, asking the questions, "How do trail building and presence affect terrestrial wildlife site use at the population level?" and "How do trail building and presence affect terrestrial wildlife site use at the community level ?" Our results showed impacts at both the population- and community-level. These impacts were primarily confined to the trail building phase, with less substantial impacts found in the terrestrial vertebrate community during the first three months after trail building was complete. Our results support the coexistence of recreation and wildlife in temperate forest ecosystems.

Summary of findings

In the first section of this dissertation, we developed a method to quantify human activity along trails. We found that camera position was important in improving the accuracy of observations, with the optimal camera position including three criteria: (1) locations where trail users move at approximately 8 kph or slower, (2) oriented at an angle of 20-degrees to the direction of movement, and (3) placed 1-2m from the trail edge. Using these criteria, we found that pedestrians were captured with at least 75% reliability by both commonly used camera models, while cyclists were more reliably captured by Reconyx cameras than by Bushnell cameras. However, we found the method had low reliability in determining demographic information. These findings were consistent with previous studies using camera traps to quantify human trail-based activity (Fairfax et al., 2012). The method we developed adds the capacity to quantify humans and wildlife simultaneously along trails through incorporating methodological recommendations from wildlife researchers (Kays & Slauson, 2008; Rowcliffe et al., 2011; TEAM Network, 2011). We concluded that using these guidelines, trail-based human and wildlife activity can be captured reliably and simultaneously using camera traps.

Implementing this method in a BACI experimental design along an equestrian trail, we found species-specific attraction and avoidance to the on-trail and near-trail zones, primarily during trail building. Raccoons were attracted to the trail while coyotes and deer avoided this area during trail building. After trail building, squirrels avoided the on-trail zone. Our community-level analysis suggested that species richness increased substantially during trail building in the on-trail zone and decreased slightly after trail building in the near-trail zone. Mesopredators were more active during and after than before trail building, while larger predators had decreased activity levels in the on-trail and near-trail sites during and after trail building. In general, species commonly observed before trail building had reduced activity while rare species had increased activity in the on-trail and near-trail zones during and after trail building. Community-level shifts were stronger during trail building than after the completion of the trail.

Our work contributes to the scholarship on human-wildlife interaction, revealing patterns in population- and community-level responses to the creation of a recreational trail. Results from both population- and community-level analyses were consistent with the mesopredator release hypothesis (Cove et al., 2012; Crooks & Soulé, 1999; Ordeñana et al., 2010; Prugh et al., 2009). Our results support the human shield hypothesis and also converge with findings from a BACI study which assessed the impacts of a new paved bike path parallel to a road in in Grand Tetons National Park (Chalfoun, 2011; Muhly et al., 2011; Shannon et al., 2014). Population-level attraction to and avoidance of the trail area were generally consistent with previous literature, considering the expected level of habituation to human disturbance at our study site (Engelhardt & Weladji, 2011; Erb et al., 2012; Gompper et al., 2006; Kucera, 1976; Young et al., 2015).

Limitations

Our camera trap method for collecting data on human trail users was successful for pedestrians and sometimes for cyclists, but one camera model missed a significant portion of cyclists. Additionally, the method did not prove reliable for collecting trail user demographics. The wildlife-focused camera trap setting specifications require cameras to be set relatively close to the ground (e.g. Kays & Slauson, 2008; Meek et al, 2014; Rowcliffe et al., 2011; TEAM Network, 2011), reducing the reliability of collecting demographic information, but increasing trail user privacy. In situations where demographic data is required, our camera trap method might be useable if paired with field-based calibration.

Our study of the effects of trail building on terrestrial wildlife did not include cameras placed on existing man-made trails, such as abandoned logging roads, prior to trail building. This limits our ability to differentiate between the effects of the trail structure increasing the detection probability vs. the occupancy probability. With limited resources, we could not include enough cameras on existing man-made corridors to analyze this effect. Future studies should consider stratifying the sampling design to include such structures to better parse out this effect.

However, considering these limitations, this project has produced a viable method for quantifying human-wildlife interaction along trails and contributed towards our understanding of these interactions. By implementing an experimental design, I was able to disentangle effects unrelated to the treatment, such as seasonality. This study thus contributes strong results regarding trail-based human-wildlife interaction.

Implications

The camera trap method for observing trail-based human-wildlife interactions developed in this dissertation can be implemented by managers and researchers. Our results emphasize the importance of camera positioning relative to trail traffic for accurately monitoring trail-based activity. We highly recommend calibrating the cameras through field-based observations to increase the accuracy of the method for quantifying visitor use.

The results of our case study on the impacts of trail building on the terrestrial wildlife community support the coexistence of recreation and wildlife in ecosystems similar to our study site. Alterations in both population-level and community-level effects were strongest in the trail building phase, returning to near pre-building levels after the trail was complete. The largest exceptions to this pattern were in the slightly decreased species richness in the near-trail zone and the decreased site use by eastern gray squirrel in the on-trail zone after trail building. Although the trail might result in habitat reduction for gray squirrels, this species is a habitat generalist and will likely find other suitable habitat nearby. Alternatively, if leeriness of humans is the driving factor for the reduced presence of gray squirrel near the trail site, we expect that the species will become habituated to human presence and their presence will return to pre-building levels. Likewise, if other species become habituated to the presence of the trail and the recreational activity that it brings, species richness in the near-trail zone will likely return to pre-trail levels.

In situations where new trail construction occurs in an area with endangered species, our results could have important implications. In our study, the active species richness increased by six species while two species were displaced during trail building. This increase in species richness, caused by the increased activity level of rare species, could result from decreased large predator activity, decreased competition for resources, or attraction to novel objects in the trail construction site. In areas where endangered species are rare, trail building could temporarily increase these species' activity level, possibly improving their access to resources or increasing their risk of predation from predators remaining in the area. Endangered mesopredators might experience positive effects from trail building if sympatric larger predators are pushed out of the area as found in our study. However, if species become habituated to the trail and trail-based human activity, this effect could revert to pre-trail levels.

Our study trail was designed according to sustainability guidelines, built using motorized tools, is 2m wide and compacted to sustain equestrian use, and had very light use during the post-building phase of our study. Effects of trail building and presence on the terrestrial wildlife community might be different in trails built using manual labor only, narrower trails, high-use trail areas, or along trails with different recreational use, such as mountain biking. Trail building activity could also result in displacement of endangered species if important habitat is altered during construction. To minimize the impacts of trail building on endangered species, managers can avoid planning trails which cross habitat essential to these species. Managers can also consider scheduling trail construction in months when breeding does not take place, especially for endangered species.

Future Research and Outlooks

Around the world, there are inherent conflicts in managing protected areas to conserve biodiversity while providing recreational opportunities. New research continues to expand our knowledge of human-environment interactions, discovering aspects which can lead to improved protected area management towards both of these goals. There is a great deal of research indicating that recreation in natural areas impacts the environment (Hammitt et al., 2015; Liddle, 1997). However, as we revisit research questions with new technologies, new analysis methods, and fresh perspectives, we are often able to identify factors which previously obscured patterns in these interactions. For example, a recent article revisiting the recreation ecology theory indicating a curvilinear relationship between visitor use and environmental impact argued that this pattern is overgeneralized to environmental effects which fit better with other models, such as linear or exponential models (Monz et al., 2013). In our study we developed a data collection method, implemented this method within an experimental design uncommon to this field, and found a different pattern of species richness change resulting from human activity than typically shown in previous studies. We still have a lot to learn about human-environment interactions in the recreation context.

Long-term studies using experimental approaches are needed to improve our understanding of human-wildlife interactions in recreation areas. Habitat modification, a long-term impact, is likely one of the largest impacts of trail building on wildlife (Hammitt et al., 2015; Knight & Gutzwiller, 1995). It is likely that habitat along a new trail will change in its first few years, as trails host invasive species and often have increased density of plant species (Pickering & Hill, 2007). There is also a need for controlled experiments in the field of human-wildlife interaction related to recreation. This type of study has been implemented in other areas of recreation ecology, leading to the development of use-impact theories in this field. Research methods for human-wildlife interaction and recreation ecology continue to improve. Technological advances in data collection methods such as GPS, radio telemetry, field cameras, accelerometers, and numerous other sensors allow researchers to collect long-term data in remote locations. The increasing availability of these data makes implementing experimental designs more accessible. Many of these methods can collect data on multiple aspects of natural resource research and management simultaneously, improving the overall management of protected areas while advancing our understanding of the impacts of recreation on the environment.

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APPENDICES

Appendix A. Supplement to Chapter 3

As part of my analysis, I performed dredging to determine the most important covariates for each occupancy model. The results were very similar and I determined that each covariate was important for the interpretation of the results, so I chose to present results for the full model. The results for relative variable importance ranking based on the full set of models are provided in Table A.1. Having decided to retain all covariates in occupancy modelling, I kept the same covariates in regression analysis since these covariates are important for the interpretation of the results.

Table A.1. Relative variable importance for zone-phase, season, and detection distance covariates. Those with importance ranking less than 0.50 are highlighted in red.

	Relative variable importance					
	Count			Zero		
	Zone*Phase	Season	Detection Distance	Zone*Phase	Season	Detection Distance
Deer	1.00	1.00	1.00	1.00	1.00	1.00
Squirrel	1.00	1.00	0.53	1.00	0.69	0.34
Raccoon	1.00	1.00	0.49	0.99	1.00	0.34
Coyote	0.83	0.46	0.93	0.25	0.91	0.45
Turkey	0.99	0.94	0.97	0.50	0.64	1.00

Occupancy code:

```
install.packages("RMark")
install.packages("MuMIn")
library(RMark)
library(MuMIn)


#Load data
SPEC <- read.table("C:/.../Coyo.txt",
header=TRUE,colClasses=c(rep("character",6),rep("numeric",5),rep("characte
r",40)))
```

```
for (i in 11:51) {
  SPEC[SPEC[,i]==".",i]="0"
  SPEC[,i]=as.numeric(SPEC[,i]) }
SPEC$Zone <- factor(SPEC$Zone)
SPEC$DetectionDist <- as.numeric(SPEC$DetectionDist)
SPEC$Season2 <- SPEC$Season2
SPEC$Phase <- factor(SPEC$PhaseZDO)

#Create data subsets to answer the specific research questions
bact <- subset(SPEC, SPEC$Zone!="F" & SPEC$PhaseZDO!="D" )
bdct <- subset(SPEC, SPEC$Zone!="F" & SPEC$PhaseZDO!="O" )
bacf <- subset(SPEC, SPEC$Zone!="T" & SPEC$PhaseZDO!="D" )
bdcf <- subset(SPEC, SPEC$Zone!="T" & SPEC$PhaseZDO!="O" )

#General model for occupancy estimates
SPEC.models.X=mark(SPEC, model="Occupancy", group=c("Zone", "Phase"),
model.parameters=list(
   p=list(formula=~DetectionDist+Season2),
   Psi=list(formula=~Zone*Phase)), invisible=FALSE)

#This gives an interaction term Zone*Phase, which shows if the data
supports a significant effect of the treatment. If the confidence interval
includes zero, it is not significant (calculate p-value from CI).
SPEC.models.bactX=mark(bact, model="Occupancy", group=c("Zone", "Phase"),
model.parameters=list(
   p=list(formula=~DetectionDist+Season2),
   Psi=list(formula=~Zone*Phase)), invisible=FALSE)
SPEC.models.bacfX=mark(bacf, model="Occupancy", group=c("Zone", "Phase"),
model.parameters=list(
   p=list(formula=~DetectionDist+Season2),
   Psi=list(formula=~Zone*Phase)), invisible=FALSE)
SPEC.models.bdctX=mark(bdct, model="Occupancy", group=c("Zone", "Phase"),
model.parameters=list(
   p=list(formula=~DetectionDist+Season2),
   Psi=list(formula=~Zone*Phase)), invisible=FALSE)
SPEC.models.bdcfX=mark(bdcf, model="Occupancy", group=c("Zone", "Phase"),
model.parameters=list(
   p=list(formula=~DetectionDist+Season2),
   Psi=list(formula=~Zone*Phase)), invisible=FALSE)


#Plot Psi with error bars (replace file name and yaxis label for each of
the five species)
require(ggplot2)

occup <- read.csv("C:/.../Coyo.csv", header=TRUE, sep = ",")
Zone = factor(occup$Zone)
Phase = factor(occup$Phase)
occu = as.numeric(occup$Psi)
low = as.numeric(occup$Lower)
upp = as.numeric(occup$Upper)
```

```
pd <- position_dodge(0.1)
limitsCI = aes(ymax = occup$Upper, ymin = occup$Lower)
limitsSE = aes(ymax=occu+occup$SE, ymin=occu-occup$SE)
limitsSEC = aes(ymax=occu+occup$SECorr, ymin=occu-occup$SECorr)
std = as.numeric(occup$SE)
ggplot(occup, aes(x=Phase, y=occu, colour=Zone)) + geom_errorbar(limitsSE,
width=0.1, position=pd) + geom_point(stat="identity", position=pd) +
geom_line(aes(group=Zone), position=pd) + labs(y="Turkey Psi") +
scale_colour_manual(values=c("#999999", "#56B4E9", "#33CC00"),
                      name="Experimental\nZone",
                      breaks=c("On-Trail", "Off-Trail", "Control"),
                      labels=c("On-Trail", "Near-Trail", "Control"))
```

Detection rate code:

```
require(pscl)
require(lsmeans)

#This dataset has a line for each camera trap day, including zeros.
zinb <- read.csv("C:/.../CCD_AllSpecies.csv",header=TRUE)

#Zero-inflated Poisson (ZIP) Model
summary(m1 <- zeroinfl(Deer ~
    ZP+DetectionDist+Season|ZP+DetectionDist+Season, data = zinb))

#Calculate least square means from the ZIP model, using the mean of
"count" and "zero" portions of the ZIP results
summary(result.zone<-lsmeans(m1, "ZP", mode="mean"))

#Perform contrasts using the results from least square means
contrast(result.zone, list(bact=c(-1,0,1,0,0,0,1,0,-1)))
confint(contrast(result.zone, list(bact=c(-1,0,1,0,0,0,1,0,-1))))
contrast(result.zone, list(bacf=c(-1,0,1,1,0,-1,0,0,0)))
confint(contrast(result.zone, list(bacf=c(-1,0,1,1,0,-1,0,0,0))))
contrast(result.zone, list(bdct=c(-1,1,0,0,0,0,1,-1,0)))
confint(contrast(result.zone, list(bdct=c(-1,1,0,0,0,0,1,-1,0))))
contrast(result.zone, list(bdcf=c(-1,1,0,1,-1,0,0,0,0)))
confint(contrast(result.zone, list(bdcf=c(-1,1,0,1,-1,0,0,0,0))))


#Plot lsmeans with error bars (replace file name and y-axis label for each
of the five species)
require(ggplot2)
full<- read.csv("C:/.../Coyo.csv", header=T)
pd <- position_dodge(0.1)
lsmean<-as.numeric(full$lsmean)
se<-as.numeric(full$SE)
ggplot(full, aes(x=Phase, y=lsmean, colour=Zone, group=Zone)) +
geom_errorbar(aes(ymin=lsmean-se, ymax=lsmean+se), width=.1, position=pd)
+ geom_line(position=pd) + geom_point(position=pd) + labs(y="Turkey
lsmeans") + scale_colour_manual(values=c("#999999", "#56B4E9", "#33CC00"),
```

```
                       name="Experimental\nZone",
                       breaks=c("On-Trail", "Off-Trail", "Control"),
                       labels=c("On-Trail", "Near-Trail", "Control"))
```

Figure 3.3

```
#Plot species richness
#Plot lsmeans with error bars
require(ggplot2)
speciesrichness<- read.csv("C:/.../SpeciesRichnessR.csv", header=T)
pd <- position_dodge(0.1)
Zone <- factor(speciesrichness$Zone)
specrich<-as.numeric(speciesrichness$RelativeSpeciesRichness)
ggplot(speciesrichness, aes(x=Phase, y=specrich, colour=Zone)) +
geom_line(aes(group=Zone), position=pd) + geom_point(position=pd) +
labs(y="Species per unit effort,\nstandardized to control zone") +
scale_colour_manual(values=c("#56B4E9", "#33CC00"),
                       name="Experimental\nZone",
                       breaks=c("On-Trail", "Off-Trail"),
                       labels=c("On-Trail", "Near-Trail"))
```

Appendix B. Supplement to Chapter 4

Table B.1. Detections of each species by phase and zone, standardized to effort by multiplying the raw number of detections by average effort, divided by effort for the zone/phase dataset. Effort was measured in camera trap days.

	Before			During			After		
Species	Control	Near-Trail	On-Trail	Control	Near-Trail	On-Trail	Control	Near-Trail	On-Trail
Wildlife Activity									
White-tailed Deer	954.9	1047.3	996.0	572.0	342.8	447.6	277.8	396.0	422.8
Gray Squirrel	68.4	157.9	182.4	69.6	180.1	80.5	118.9	175.4	89.4
Northern Raccoon	33.8	113.5	75.8	12.5	64.4	158.8	80.0	126.6	108.7
Coyote	36.1	41.4	45.8	59.2	4.4	19.8	12.9	4.6	19.3
Wild Turkey	28.4	15.3	44.0	38.4	10.9	3.3	1.2	22.1	21.7
Virginia Opossum	14.6	11.5	6.5	20.8	16.4	19.8	29.4	27.9	16.9
Mouse or Rat	11.5	8.4	2.8	21.8	19.7	0.0	35.3	1.2	4.8
American Black Bear	9.2	3.8	2.8	8.3	2.2	6.6	28.3	19.7	4.8
Striped Skunk	13.8	3.8	3.7	13.5	6.6	2.2	25.9	3.5	1.2
Bobcat	3.1	5.4	2.8	9.3	0.0	4.4	10.6	5.8	8.5
Eastern Cottontail	8.5	0.8	0.0	13.5	0.0	0.0	5.9	0.0	0.0
Southern Flying Squirrel	6.1	2.3	2.8	0.0	1.1	1.1	1.2	0.0	0.0
Gray fox	4.6	1.5	0.0	0.0	0.0	2.2	0.0	0.0	2.4
Red Fox	1.5	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eastern Spotted Skunk	0.0	0.0	0.0	0.0	1.1	1.1	0.0	0.0	0.0
Eastern Fox Squirrel	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0
Long-tailed Weasel	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0
Woodchuck	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0
Trail Building & Recreational Activity									
Human	27.7	0.0	4.7	2.1	1.1	1145.5	1.2	10.5	1700.9
Domestic Horse	0.0	0.0	0.0	0.0	0.0	11.0	0.0	10.5	1436.3
Vehicle	0.0	0.0	0.0	0.0	63.3	948.2	0.0	1.2	35.0
Domestic Dog	0.8	0.0	0.0	0.0	0.0	71.7	0.0	2.3	85.8
Bicycle	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.2

Table B.2. Difference in the change of detection rate (number of detections per camera trap day) between phases in each treatment site, minus the same change in the control site for each study species. Red highlighting indicates species whose detection rate decreased more in the treatment zone than the control zone; green highlighting indicates species whose detection rate increased more in the treatment zone than the control zone, and yellow highlighting indicates species whose change in detection rate did not differ between treatment and control zones (change in detection rate between -0.001 and 0.001 detections per camera trap day). Italicized species had only one observation in the study.

Trophic Group	**Predator/ Prey Group**	**Species**	**During/ Near-trail**	**During/ On-trail**	**After/ Near-trail**	**After/ On-trail**
Carnivore	Large Predator	Coyote	-0.077	-0.063	-0.017	-0.004
		Bobcat	-0.015	-0.006	-0.009	-0.002
	Small Predator	*Long-tailed Weasel*	*0*	*0*	*0.001*	*0*
	Meso-predator	Red F ox	0.001	0.002	0.001	0.002
		Gray fox	0.004	0.009	0.004	0.009
Herbivore	Prey	White-tailed Deer	-0.411	-0.212	0.033	0.133
		Eastern Gray Squirrel	0.027	-0.132	-0.042	-0.183
		Wild Turkey	-0.018	-0.065	0.043	0.006
		Mouse or Rat	0.001	-0.017	-0.04	-0.028
		Eastern Cottontail	-0.007	-0.006	0.002	0.003
		Eastern Fox Squirrel	*0*	*-0.001*	*0*	*-0.001*
		Woodchuck	*0*	*0.001*	*0*	*0*
		Southern Flying Squirrel	0.006	0.006	0.003	0.003
Omnivore	Small Predator	Striped Skunk	0.004	-0.002	-0.016	-0.019
		Eastern Spotted Skunk	*0.001*	*0.001*	*0*	*0*
	Neither	American Black Bear	-0.001	0.006	-0.004	-0.022
	Meso-predator	Virginia Opossum	-0.002	0.009	0.002	-0.006
		Northern Raccoon	-0.035	0.133	-0.042	-0.017

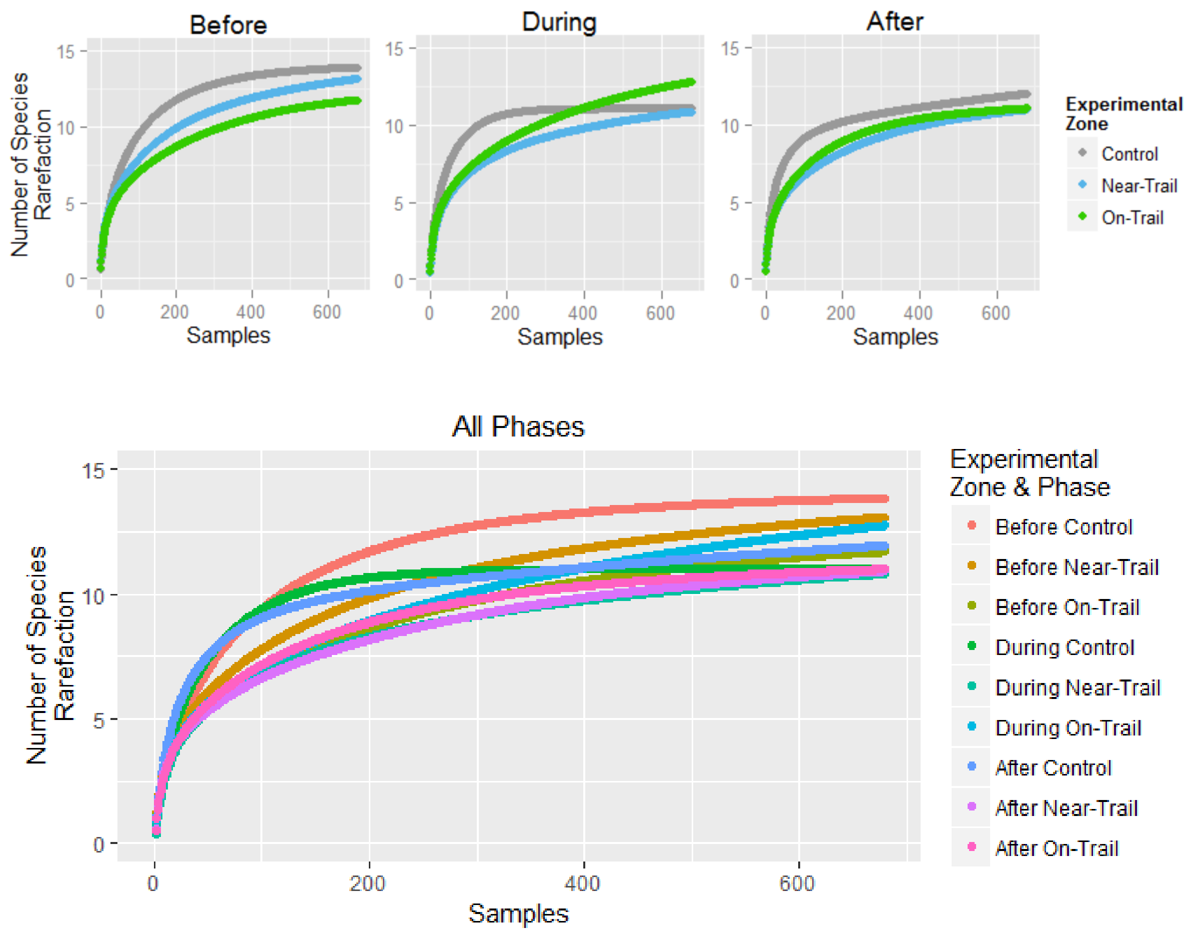

Figure B.1. Sample-based rarefaction values for each zone during each phase of the project. We observe that for nearly all data subsets, the accumulation curve does not reach an asymptote, suggesting that there are more species in the area than were observed with camera traps. For this reason, we chose to use the Chao1 species richness estimator. Each sample is cut off at 679 surveys, the largest number of camera trap days for the smallest survey period (after/control).

R Code for graphics

```
require("ggplot2")
```

Figure 4.1

```
chao1 <- read.csv("C:/.../Chao1.csv", header=TRUE)

#Plot Chao1 Estimator
pd <- position_dodge(0.1)
pB <- ggplot(chao1, aes(x)) + theme(legend.position="none") +
     geom_point(aes(x=BCSamples, y=BCChao.1.Mean, colour = "Control"))  +
     geom_point(aes(x=BFSamples, y=BFChao.1.Mean, colour = "Off-Trail"))  +
     geom_point(aes(x=BTSamples, y=BTChao.1.Mean, colour = "On-Trail"))  +
     xlab("Samples, Before Trail Building") + ylab("Number of Species\nChao1
Estimator") +
     geom_vline(xintercept = 679) +
     xlim(0, 750) + ylim(0,17) +
     scale_colour_manual(values=c("#999999", "#56B4E9", "#33CC00"),
                         name="Experimental\nZone",
                         breaks=c("On-Trail", "Off-Trail", "Control"),
                         labels=c("On-Trail", "Near-Trail", "Control"))


pD <- ggplot(chao1, aes(x)) + theme(legend.position="none") +
     geom_point(aes(x=DCSamples, y=DCChao.1.Mean, colour = "Control"))  +
     geom_point(aes(x=DFSamples, y=DFChao.1.Mean, colour = "Off-Trail"))  +
     geom_point(aes(x=DTSamples, y=DTChao.1.Mean, colour = "On-Trail"))  +
     xlab("Samples, During Trail Building") + ylab("Chao1 Estimator") +
     geom_vline(xintercept = 679) +
     xlim(0, 750) + ylim(0,17)+
     scale_colour_manual(values=c("#999999", "#56B4E9", "#33CC00"),
                         name="Experimental\nZone",
                         breaks=c("On-Trail", "Off-Trail", "Control"),
                         labels=c("On-Trail", "Near-Trail", "Control"))

pO <- ggplot(chao1, aes(x)) + theme(legend.title=element_blank()) +
     geom_point(aes(x=OCSamples, y=OCChao.1.Mean, colour = "Control"))  +
     geom_point(aes(x=OFSamples, y=OFChao.1.Mean, colour = "Off-Trail"))  +
     geom_point(aes(x=OTSamples, y=OTChao.1.Mean, colour = "On-Trail"))  +
     xlab("Samples, After Trail Building") + ylab("Chao1 Estimator") +
     geom_vline(xintercept = 679) +
     xlim(0, 750) + ylim(0,17) +
     scale_colour_manual(values=c("#999999", "#56B4E9", "#33CC00"),
                         name="Experimental\nZone",
                         breaks=c("On-Trail", "Off-Trail", "Control"),
                         labels=c("On-Trail", "Near-Trail", "Control"))
```

Figure 4.2

```
controlled <- read.csv("C:/.../Chao1_679.csv", header=TRUE)

limitsC <- aes(ymin=Chao.Lower, ymax=Chao.Upper)
pd <- position_dodge(0.1)

pLineC <- ggplot(controlled, aes(x=Phase, y=Chao1, colour=Zone)) +
geom_point(position=pd) + geom_errorbar(limitsC, width=.1, position=pd) + ylim(-
2.5,5) + geom_line(aes(group=Zone), position=pd) + ylab("Active Species
Richness,\nControlled") + geom_hline(yintercept = 0) +
     scale_x_discrete(name = "Phase", limits=c("Before","During","After")) +
     scale_colour_manual(values=c("#56B4E9", "#33CC00"),
                        name="Experimental\nZone",
                        breaks=c("On-Trail", "Off-Trail"),
                        labels=c("On-Trail", "Near-Trail"))
```

Figure 4.3

```
chao <- read.csv("C:/.../ColemansRarefaction_withoutRep_100rep_ClassicChao.csv",
header=TRUE)

pBoxC <- ggplot(chao, aes(x=Phase, y=Chao1, fill=Zone)) +
     geom_bar(stat="identity", position=position_dodge()) +
     scale_fill_manual(values=c("#56B4E9", "#33CC00")) +
     geom_errorbar(limitsC, width=.1, position=position_dodge(.85)) +
     ylab("Active Species Richnes,\nContrast") +
     geom_hline(yintercept = 0) +
     geom_text(aes(label=Chao1), size=4, vjust=-1, position=position_dodge(.9)) +
     scale_x_discrete(name = "Phase", limits=c("During","After")) +
     ylim(-3, 8) +
     scale_fill_manual(values=c("#56B4E9", "#33CC00"),
                        name="Experimental\nZone",
                        breaks=c("On-Trail", "Off-Trail"),
                        labels=c("On-Trail", "Near-Trail"))
```

Figure B.1

```
coleman <- read.csv("C:/.../Chao1.csv", header=TRUE)

p.estB <- ggplot(coleman, aes(x)) +
     geom_point(aes(x=BCSamples, y=BCS.est., colour = "Before Control"))  +
     geom_point(aes(x=BFSamples, y=BFS.est., colour = "Before Off-Trail"))  +
     geom_point(aes(x=BTSamples, y=BTS.est., colour = "Before On-Trail"))  +
     labs(title = "Before", x="Samples", y="Number of Species\nRarefaction", colour="Zone") +
     scale_colour_manual(values=c("#999999", "#56B4E9", "#33CC00"),
           name="Experimental\nZone",
           breaks=c("Before Control", "Before Off-Trail", "Before On-Trail"),
          labels=c("Control", "Near-Trail", "On-Trail")) +
     ylim(0,15) + xlim(0,680)

p.estD <- ggplot(coleman, aes(x)) +
     geom_point(aes(x=DCSamples, y=DCS.est., colour = "During Control"))  +
     geom_point(aes(x=DFSamples, y=DFS.est., colour = "During Off-Trail"))  +
     geom_point(aes(x=DTSamples, y=DTS.est., colour = "During On-Trail"))  +
     labs(title = "During", x="Samples", y="Number of Species\nRarefaction", colour="Zone") +
     scale_colour_manual(values=c("#999999", "#56B4E9", "#33CC00"),
           name="Experimental\nZone",
           breaks=c("During Control", "During Off-Trail", "During On-Trail"),
          labels=c("Control", "Near-Trail", "On-Trail")) +
     ylim(0,15) + xlim(0,680)
```

```
p.estA <- ggplot(coleman, aes(x)) +
     geom_point(aes(x=OCSamples, y=OCS.est., colour = "Open Control"))  +
     geom_point(aes(x=OFSamples, y=OFS.est., colour = "Open Off-Trail"))  +
     geom_point(aes(x=OTSamples, y=OTS.est., colour = "Open On-Trail"))  +
     labs(title = "After", x="Samples", y="Number of Species\nRarefaction", colour="Zone") +
     scale_colour_manual(values=c("#999999", "#56B4E9", "#33CC00"),
           name="Experimental\nZone",
           breaks=c("Open Control", "Open Off-Trail", "Open On-Trail"),
          labels=c("Control", "Near-Trail", "On-Trail")) +
     ylim(0,15) + xlim(0,680)

p.est <- ggplot(coleman, aes(x)) +
     geom_point(aes(x=BCSamples, y=BCS.est., colour = "Before Control"))  +
     geom_point(aes(x=BFSamples, y=BFS.est., colour = "Before Off-Trail"))  +
     geom_point(aes(x=BTSamples, y=BTS.est., colour = "Before On-Trail"))  +
     geom_point(aes(x=DCSamples, y=DCS.est., colour = "During Control"))  +
     geom_point(aes(x=DFSamples, y=DFS.est., colour = "During Off-Trail"))  +
     geom_point(aes(x=DTSamples, y=DTS.est., colour = "During On-Trail"))  +
     geom_point(aes(x=OCSamples, y=OCS.est., colour = "Open Control"))  +
     geom_point(aes(x=OFSamples, y=OFS.est., colour = "Open Off-Trail"))  +
     geom_point(aes(x=OTSamples, y=OTS.est., colour = "Open On-Trail"))  +
     labs(title = "All Phases", x="Samples", y="Number of Species\nRarefaction") +
     scale_colour_discrete(name = "Experimental\nZone & Phase",
           breaks=c("Before Control", "Before Off-Trail", "Before On-Trail",
                    "During Control", "During Off-Trail", "During On-Trail",
                    "Open Control", "Open Off-Trail", "Open On-Trail"),
           labels=c("Before Control", "Before Near-Trail", "Before On-Trail",
                    "During Control", "During Near-Trail", "During On-Trail",
                    "After Control", "After Near-Trail", "After On-Trail")) +
     geom_vline(xintercept = 679)
```