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ESTIMATING FURBEARER DENSITY USING TRAIL-CAMERAS AT THE PIEDMONT NATIONAL WILDLIFE REFUGE, GEORGIA

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**ESTIMATING FURBEARER DENSITY USING TRAIL-CAMERAS AT THE
PIEDMONT NATIONAL WILDLIFE REFUGE, GEORGIA**

by

PATRICK MCMILLAN POWERS

B.S., Georgia College and State University, 2018

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College of Arts and Sciences
Department of Biological and Environmental Sciences

We hereby approve the thesis of

**ESTIMATING FURBEARER DENSITY USING TRAIL-CAMERAS AT THE
PIEDMONT NATIONAL WILDLIFE REFUGE, GEORGIA**

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ABSTRACT

Density estimation is an important indicator of the health of wildlife populations and is commonly used to establish management practices. Trail-cameras offer a unique advantage in the density estimation of elusive animals as data can be collected without the need for physical capture. The objectives of this study were to estimate and compare furbearer density between two major habitats at the Piedmont National Wildlife Refuge (PNWR) and to compare computed density values from paired cameras located at off- and on-road locations. An additional goal was to assess the usefulness of trail-cameras as a viable technique to estimate population density on the refuge. Trail-camera monitoring took place from April to September of 2019. Density estimates for five furbearer species were calculated using a model developed for animals not uniquely identifiable. Virginia opossums were the most frequently observed furbearer, followed by coyotes, raccoons, bobcats, and gray foxes. Average density estimates between bottomland and upland habitats did not differ significantly among all observed species. Values obtained at off- and on-road locations in upland habitat was significantly different only for the coyote ($p=0.02$). Density estimates in bottomland were not significantly different than on-road locations in upland areas for opossum, raccoon, and gray fox ($p= 0.89, 0.13, 0.15$), however, coyote and bobcat estimates were significantly higher at on-road locations ($p=0.001, 0.04$). A comparison of habitat and elevation was largely insignificant across species, except for raccoons ($p=0.04$). Data collected for this species suggested lower elevation areas had higher density levels. Camera deployment and monitoring was laborious and time consuming. Wildlife officials aiming to collect population data on opossums and gray foxes should consider placing cameras directly on roads as it is less labor intensive and provides similar density estimates between habitats. For raccoons, elevation may be a better indicator of density, with higher values observed at lower

elevations. Cameras monitoring raccoons should be placed on roads with different elevations. Cameras used to monitor bobcats and coyotes should be located off-road to ensure a more representative sample. For general species monitoring, on-road camera placement would be sufficient as all observed species were seen at least once at these locations.

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INTRODUCTION

Furbearing Animals

There are over 4200 species of mammals worldwide, but only 27 are considered furbearers (White et al. 2015). A furbearer refers to a species of mammal whose skin is commercially valuable (White et al. 2015). In general, furbearers are extremely adaptable, often occupying both rural forested and urban areas. Home ranges vary greatly among species, from a few hectares to many thousand. White et al. (2015) recently reviewed the history of furbearers in North America. These animals were first hunted by prehistoric people more than 11,000 years ago. Pre-colonial trapping methods were primitive and had little effect on numbers. Populations appear to have remained stable up until the 1500s, when European settlers arrived. Unregulated harvesting by colonists quickly resulted in great reductions or extinction of once common furbearer species such as the American beaver (*Castor canadensis*) and sea mink (*Neovison macrodo*, extinct by the early 1900's). The recognition of these declines prompted the first regulations to be enacted in the 1600s. These conservation efforts created a more controlled harvest system, helping some populations recover.

The eastern United States is home to a number of different furbearing mammals that live in sympatry and vary in abundance (Kelly and Holub 2008, Chamberlain and Leopold 2005, Moruzzi et al. 2002). Southeastern species include: muskrat (*Ondatra zibethicus*), river otter (*Lontra canadensis*), beaver, striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), black bear (*Ursus americanus*), and opossum (*Didelphis virginiana*) (White et al. 2015). Coyotes and black bears occupy the highest trophic levels in the southeast whereas beavers, muskrats, and opossums occupy lower levels (White et al. 2015). Species in higher trophic levels

tend to be found in lesser abundance than ones in lower levels. Beavers and muskrats are examples of habitat specific taxa requiring streams or low-lying areas that hold water (Baker and Hill 2003, Erb and Perry 2003). Other species such as coyote and bobcats are cosmopolitan, occupying a variety of different habitats.

In the past century, carnivorous furbearer abundance has increased considerably. Prugh et al. (2009) termed this phenomenon “mesopredator release” and described it as an increase in the abundance of medium-sized mammalian carnivores due to the absence of larger carnivores. The process is defined more broadly as the expansion in density or distribution of a middle-ranked predator ranging in size from 1.0 to 15.0 kg (Gehrt and Clark 2003). Coyotes serve as an example of a mesopredator in the southeastern United States. These animals were once confined to arid regions in the western half of the continent but have undergone a dramatic range expansion since 1900 (Hody and Kays 2018). This is attributed to land conversion and the absence of apex predators (Prugh et al. 2009). In urban settings, coyotes have adapted exceptionally well because of the food availability.

Numerous other factors have contributed to the recent success of additional furbearer species (e.g. raccoons, bobcats, and opossums). The extirpation of apex predators such as the mountain lion (*Puma concolor*) and red wolf (*Canis lupus rufus*) has reduced the predation risk and allowed for smaller furbearers to expand their range (White et al. 2015). Apex predators typically occupy large areas, making them more vulnerable to the negative effects of habitat fragmentation, thereby making them more likely to disappear. In connection with habitat fragmentation, urban development and newly created agricultural lands have aided in the expansion of medium-sized furbearers, adding to the available resources, such as crops, pet food, and garbage. In addition to these contributing factors, animal activism groups targeting highly

regulated wildlife harvest programs have influenced trapping regulations and, in some cases, convinced government agencies to restrict or eliminate the harvesting of furbearers (White et al. 2015). The increase in medium-sized furbearers has had negative consequences for some organisms. For example, Schmidt (2003) found nest predation from increased raccoon populations was having significant impacts on songbird populations in Illinois. Kilgo et al. (2012) found predation by coyotes was the greatest source of fawn mortality in white-tailed deer (*Odocoileus virginianus*) neonates in South Carolina.

Many common furbearers (e.g. coyotes, raccoons bobcats, foxes) have sympatric distributions (Neale and Sacks 2001, Chamberlain and Leopold 2005; Conway et al. 2015). Neale and Sacks (2001) investigated the interspecific relationship of food habits and space use between sympatric populations of gray foxes, coyotes, and bobcats. Scat collection and spatial analysis revealed a high degree overlap between all species. The authors noted that population sizes among gray foxes, coyotes, and bobcats, could fluctuate significantly if food shortages became prevalent. Chamberlain and Leopold (2005) also studied the spatial distribution of gray foxes, coyotes, and bobcats, finding all species shared home ranges and selected similar prey items during some seasons. Coyotes and foxes were found to have more similar diets, resulting in the potential for increased resource competition. Bobcat and gray fox diets were less similar, implying competition for food resources may be less. Lastly, a review of the trends in Mississippi predator populations found increasing coyote populations will likely keep bobcat and red and gray fox populations from expanding due to increased spatial and food resource competition (Prugh et al. 2009).

Monitoring methods

Managing furbearer populations is important as their numbers can influence the abundance of other wildlife species. Modern furbearer management has become critical in ensuring sustainability of future wildlife populations as well as protecting human health and property (White et al. 2015). Harvest limits related to furbearers often change on a yearly basis so scientifically based programs have been implemented to monitor and regulate populations. Species are difficult to monitor due to their elusive behavior, often nocturnal habits, and low density across the landscape. Traditional methods used to estimate furbearer populations came from harvest records submitted by hunters and trappers. Harvest data is still used to estimate population parameters, but many present-day studies now employ non-harvest methods. Non-lethal harvest methods, excluding trail-camera systems, include: scent stations (Conner et al. 1983), track counts (D'Eon 2001, Magoun et al. 2006, Darren et al. 2008), scat collections (Neale and Sacks 2001), hair snags (Downey et al. 2006), mark and recapture (Babb and Kennedy 1989), siren-response surveys (Lovell et al. 1998), and radio-telemetry (Dellinger et al. 2018). Scent stations have been used extensively in the past, and often in combination with other methods. Scent-stations employ a lure, usually in the form of another animals' urine, to attract different species. Domesticated cat, coyote, and bobcat urine are the most commonly used scent lures in furbearer studies (Conner et al. 1983, Sarmiento et al. 2009, Pyrah 1984).

Since furbearers have distinctive tracks, they can be detected by the footprints they leave behind in deformable substrates. Track counts can be performed in two ways. First, researchers can create a soft substrate at a specific location that will allow for any animal track to be imprinted on the ground; a scent station is typically used in conjunction with this method in order to attract animals to the substrate location. In the second method, the track count technique simply entails actively looking for tracks within a study area.

The mark-recapture method is likely the oldest and most traditional data collection method still in use. For this method, animals are captured, marked, and released. After a period of time, trapping takes place again. Any recaptured individuals that were marked during the first capture are recorded and later used to make estimations on the population size. Live-trapping techniques used for mark-recapture studies include foot hold traps, cage traps, and wire snares. Mark-recapture methods are also used in trail-camera studies to gather data on uniquely identifiable animals (Bashir et al. 2013, Martorello et al. 2001, Heilbrun et al. 2006). For more in-depth spatial studies, radio telemetry is often employed.

Additional techniques used for gathering data include scat collection, hair snags and siren response surveys. An analysis of scat can give insight on an animal's diet and allow for the estimation of biomass being consumed. Scat collection is often used in conjunction with other survey methods and is valuable in determining the presence of dietary overlap between species (Neale and Sacks 2001). Hair snags, often made of wire, are a simple way to collect small amounts of hair off a passing animal to determine species presence. Hair samples can then be analyzed to generate a genetic profile of the targeted species (Downey et al. 2006). Siren response surveys are less commonly used but can still provide information on abundance and distribution within a specific area based on the number and directions of responses. This method is most often used on coyotes (Lovell et al. 1998).

Trail-Camera Basics

Motion-detection cameras, often referred to as "trail cameras", have been used worldwide for the study of species presence, population estimates, habitat selection, and behavioral patterns (Sarmiento et al. 2009, Symmank et al. 2014, Mcfadden-Hiller and Hiller 2015, Sirén et al. 2016). Trail-cameras have become a commonly used tool for field biologists as they offer a unique

advantage in the monitoring of an animal without physical capture. The first commercially available camera traps were used in the 1980s (Rovero et al. 2013). During this time, units typically consisted of an off-the-shelf camera that was programmed to capture an image when an infrared beam was broken (Figure 1). Newer models, however, are much more dependable and sophisticated. Some units are even equipped with cellular capabilities that can instantly send a image or video to a computer or cell phone (Scheideman et al. 2017). Camera systems can be relatively inexpensive, but with many optional features available, prices (U.S.) range from less than \$200 to more than \$600 (Scheideman et al. 2017).

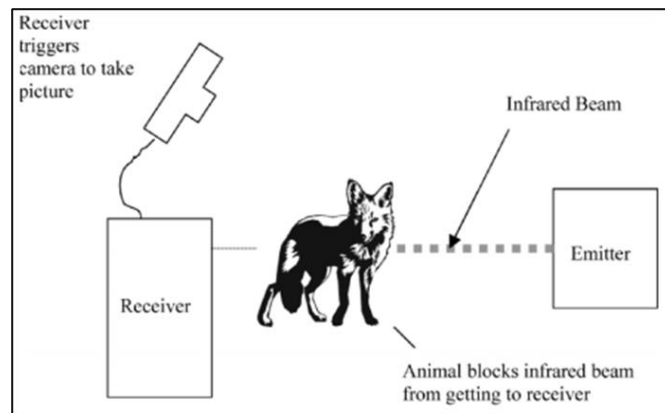


Figure 1: Active infrared camera system configuration (Swann et al. 2004).

Current trail-cameras use infrared technology, with either an “active” or “passive” infrared light system (Swann et al. 2004). Active systems emit an invisible beam of infrared light to a separate receiver (Figure 1) which sends a signal to the camera to capture an image when an animal crosses the beam. Passive systems are the most often used camera system for present day studies as the capture field is wider (McCallum 2013). These systems detect differences in the ambient background heat given off by a moving animal (Figure 2). The heat difference between the background and the animal triggers the camera to take a photograph. Passive systems generally emit a wide band of infrared light. As opposed to a single beam, the larger band allows for wider detection zone, thereby making it more likely to capture an animal (Figure 2).

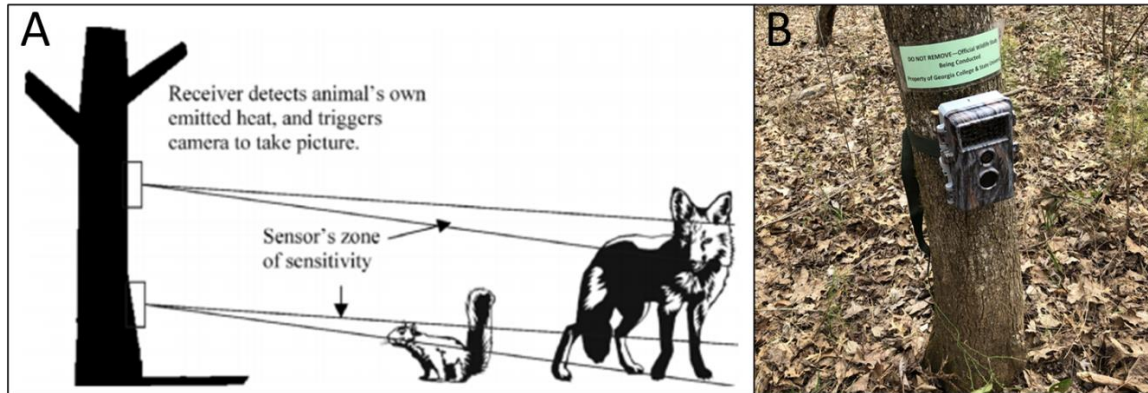


Figure 2: (A) Passive infrared camera configuration (Swann et al. 2004); (B) Passive infrared camera unit used in the PNWR study.

Rovero et al. (2013) described the additional specifications that come standard on all trail-cameras. The previously mentioned detection zone feature is the area in which a camera is able to detect a target. This is not necessarily equal to the camera's field of view, meaning an animal can be within the zone of detection, but out of photographic range. This most often occurs in heavily forested areas as a camera unit may detect a target but fail to produce a useful image due to dense vegetation obscuring the field of view. Trigger-speed is another fundamental feature that varies between units and is critical in the capturing of an image. The trigger-speed is the rapidity with which a camera captures an image. A "faster" trigger-speed will capture a moving target better than a "slower" trigger-speed. Infrared trail-cameras that take photographs in rapid sequence are useful for identifying animals that are moving quickly.

Cameras come equipped with a sensitivity feature that regulates the responsiveness of the camera to detect a target by changing the heat threshold. Although this setting can be adjusted, it is useful to keep the sensitivity at a higher level as it will better detect smaller sized targets. Cameras are designed to operate in poor environmental conditions and come with a durable housing and features such as automatic flash and focus, as well as the ability to attach to trees or other structures. Although capable of operating in poor conditions (e.g. high humidity, extreme

temperature, and areas with high precipitation), cameras exposed to poor weather may require more maintenance to ensure proper working order (Rovero et al. 2013).

Trail-camera studies have increased substantially in recent years (McCallum 2013). The number of camera-sites will depend on the size of the study area and rarity of the study species. Species with large home range sizes typically require more camera-sites to ensure adequate coverage (Dreibelbis et al. 2009). The use of quality cameras is critical in obtaining accurate data. Cameras should have a wide detection zone, fast trigger speed, and long-lasting power supply (Rovero et al. 2013). Although very reliable, trail-cameras can malfunction. Swann et al. (2004) found trail-cameras (especially inexpensive units) are prone to two types of errors: failure to photograph a target animal and false triggers. The latter of the two occurs when a photograph is taken, but no animal is present. False triggers may be caused by wind, rain, moving vegetation, or an animal that is inside the infrared detection zone, but outside of the cameras photographic range. Although there are some problems associated with trail-cameras, the ease of use and noninvasiveness of the devices make them a useful survey tool. Additionally, they allow for the monitoring of elusive wildlife species without the need of physical capture or handling (Kelly and Holub 2008).

Camera-trap Studies

Numerous studies in the United States have evaluated the efficacy of trail-camera use in wildlife data collection (Moruzzi et al. 2002, Kelly and Holub 2008, Symmank et al. 2014). Some studies have used trail-cameras in conjunction with traditional survey techniques to further assess camera-study validity when compared to other data collection methods. Greene et al. (2016) sampled a population of fox squirrels (*Sciurus niger*) in the southeastern United States using four different survey methods to determine which technique would be the most effective in

monitoring populations. The survey methods included camera trapping, point counts, live trapping, and line-transect surveys. All survey methods used corn as bait to attract individuals to the area. Live trapping is the most commonly used data collection method on fox squirrels, but there is much debate on its reliability. The study used two 75-ha grids that were known to be occupied by fox squirrels. Each grid contained 20 survey points spaced 250 m apart. At each survey point, a camera was placed 70 cm above the ground angled towards a bait pile. The live-trapping method placed a small wooden box trap at the base of the tree with a wire cage trap 1.5m above it. Point counts and line-transect surveys were visual methods conducted in the same grids where live-trapping took place. This study revealed that camera-traps were the most effective survey method, recording 2.65 times more detections than all other methods combined.

Mcfadden and Hiller (2015) employed the use of trail-cameras in an Oregon forest, finding that cameras were useful in detecting a variety of different animal species. This study used 60 camera units placed in different locations based on topographical and habitat features (e.g. game trails, roads, and stream areas). The authors found detection rates varied among species in regard to elevation and associated features. Another study by Moruzzi et al. (2002) found trail-cameras were sufficient in the detection of species such as raccoons, coyotes, opossums, and fishers (*Pekania [Martes] pennanti*) in a Vermont forest. Camera units were placed in 1x1 km grid pattern across a 1032 km² study area. Trail-cameras in this specific study also provided insight on species-specific habitat-use patterns. Additionally, Kelly and Holub (2008) found success in using trail-cameras to monitor carnivore species and their occurrence across the landscape in a rural Virginia forest.

Martorello et al. (2001) used trail-cameras to estimate population sizes of black bears (*Ursus americanus*). This study used mark-resite in conjunction with the camera units. Twenty

camera stations in the North Carolina wilderness captured images of marked and unmarked bears. This study revealed that trail-cameras were an effective tool in the estimation of black-bear populations. A different study conducted in East Texas monitored the activity patterns of four forest predators (bobcat, raccoon, opossum, and coyote) using infrared-triggered cameras (Symmank et al. 2014). The authors concluded that infrared triggered cameras were well suited to the task of gathering large amounts of data, with limited human effort (Symmank et al. 2014). Another study conducted by Magoun et al. (2011) used motion-detection cameras in conjunction with hair snags to determine the identity of individual wolverines (*Gulo gulo*) in southeastern Alaska. This particular study demonstrated the versatility of the trail-camera unit as temperatures ranged from -4°C to 7°C during the sampling period. Lastly, Sirén et al. (2016) used trail-cameras to estimate American marten (*Martes americana*) populations in New Hampshire. This study compared datasets obtained from camera and live-trapping methods. Density estimates and recapture rates for camera-trapping were higher and thought to be more precise as no stress related from physical capture deterred animals from the area.

Trail-cameras have also been used to estimate felid populations. A recent study of Florida panthers (*Puma concolor*) found success in using trail-cameras to identify individual panthers in Everglades National Park, Florida (McBride and Sensor 2015). This study highlighted the usefulness of trail-cameras in monitoring one of the most elusive mammalian species in the southeastern United States. Heilbrun et al. (2006) estimated bobcat abundance using a capture-recapture method with trail-cameras in southern Texas. Estimates obtained were comparable to previously reported data, indicating reliable records could be obtained without the use of physical capture and radiotelemetry. Brooks (1996) compared the effectiveness of two camera-

based systems in monitoring bobcat populations in southern Vermont, finding less expensive systems have a comparable performance to other high-priced systems.

Other trail-camera studies outside of the United States have also been performed. Sarmiento et al. (2009) used camera traps to estimate red fox (*Vulpes vulpes*) abundance in Portugal. Cameras were placed 300 to 500 m apart with the distance from each camera unit being described as the approximate diameter of the smallest home range for the species. Unlike other surveys, vegetation at camera-sites was manipulated to encourage any animal that came within camera range to approach in a lateral orientation, increasing the chance of a unique identification. The study concluded that camera-trapping was a viable tool for the estimation of red fox populations and the unique identification of individuals.

Trail-camera studies have been conducted in the rainforest as well. Line transects have been the traditional way to survey large mammalian species in tropical rainforests, but they are highly dependent on visibility. Trail-cameras have been used as a successful alternative to transects. Espartosa et al. (2011) compared the performance of camera trapping and track counts for surveying large mammals in the jungles of Brazil. An estimation of species richness and composition across the landscape revealed similar results between both methods. In addition to this study, trail-cameras have also been used in India and Africa to estimate big cat densities (Bashir et al. 2013, Brackowski et al. 2016). Gerber et al. (2010) conducted a biodiversity study in Madagascar to estimate relative abundance and density of carnivores in the eastern rainforest. Forty-three camera-trap stations were placed opportunistically along research trails with a mean distance of 494 m between neighboring units. Camera-sites were baited with chicken to increase the probability of photo-capture. Trap success (capture events/trap nights) was used to measure relative abundance in species that were not uniquely identifiable whereas capture-recapture

analyses was used to estimate population size in species that were individually identifiable. The authors noted the usefulness of the trail-camera unit, finding that it was an efficient and non-invasive tool that could be used to quantify relative abundance. Lastly, trail-cameras have also been used to monitor wildlife populations at airports. Scheideman et al. (2017) used wildlife camera traps at an airport in British Columbia to determine the presence and activity patterns of various animal species.

Trail-camera technology has made significant progress in recent years with current units having standard features that allow for reliable data collection. It is clear that camera-surveys can provide useful information regarding population size, density, habitat use, and behavioral patterns. However, care should be used when designing a trail-camera survey as there is always the potential for bias. Random camera placement is recommended, but not always necessary (Pease et al. 2016). A longer sampling effort is generally needed when cameras are randomly placed, however, inferences made at the community level are unlikely to be affected so long as surveys attain at least 1400 trap-days (Cusack et al. 2015). Mann et al. (2014) found study areas containing roads should employ a mixed design of on-and off- road camera locations to gather population data. In studies targeting specific habitat features, characteristics at site locations should be recorded as they will likely influence capture rates (Kolowski and Forrester 2015).

Furbearers in Georgia

Furbearers in Georgia often occur in sympatry as these species tend to be habitat generalists. These animals typically occur in a mixed forest ecosystem, with many species preferring areas near water sources. A notable difference among many furbearers is home range size. Although these species vary in their trophic level, dietary overlap is often present as many

have similar nutritional requirements (Neale and Sacks 2001). Most have omnivorous diets and eat a variety of different food items.

Some commonly harvested furbearer species in Georgia include bobcat, raccoon, gray fox, red fox, coyote, Virginia opossum, beaver, river otter, and muskrat. The bobcat is found in abundance throughout the state and can occupy almost any habitat type. Anderson and Lovallo (2003) found heavily forested areas are preferred, but bobcats can also be found near urban developments. Individuals usually have a primary den, but utilize auxiliary shelters such as brush piles, hollow logs, and thickets. Bobcats are primarily nocturnal hunters, feeding on rabbits and other small prey (Anderson and Lovallo 2003). Adults weigh an average of 9.6 kg and range from 47.5 to 125 cm in length (Lariviere and Walton 1997). Nowell and Jackson (1996) found that home ranges among bobcats vary significantly from 0.60 to 326.34 km² with larger ranges being found in their northern range. The average home-range size is 13 km² and although territorial, some individuals will tolerate home range overlap (Whitaker and Hamilton 1998). During the breeding season, home range sizes increase significantly, especially for males (Anderson and Lovallo 2003).

Raccoons prefer deciduous and mixed forest habitats, but their adaptability has led them occupy urban developments as well (Gehrt 2003). Vertical structures (i.e. trees, utility poles, fences) are critical in providing escape from predators, especially dogs in urban areas. Like many other furbearers, their activity is mostly nocturnal. As an omnivorous species, raccoons take advantage of a variety of different food sources such as fruits, nuts, amphibians, and bird eggs. In urban areas, food scraps make up a large proportion of their diet. Body length varies 60 to 95 cm, with males typically longer. Adult body weights range from 4.0 to 9.0 kg, depending on geographic location (Gehrt 2003). Home range size varies between males and females. In the

eastern United States, males occupy an average 3.94 km² area and females 2.44 km² (Owen et al. 2015).

Two species of fox can be found in Georgia, the gray and red fox. These animals differ in color but are similar in that they can occupy the same habitat and have similar dietary preferences. Foxes are well adapted to many different environments but prefer wooded areas. The gray fox's total body length ranges from 80 to 113 cm whereas the red fox has a body length of 68 to 75 cm. Weights are similar ranging from 3.0-8.0 kg (Cypher 2003). Home range size for the gray fox is relatively small at 3.40 km² (Deuel et al. 2017). Red foxes occupy a larger home range of 7.1 km², with size varying among habitat type, elevation, and urban development (Walton et al. 2017).

Coyotes are substantially larger than both fox species, with lengths of 100 to 130 cm. Size varies among geographic locale with males weighing an average of 13.1 and females 9.8 kg (Bekoff and Gese 2003). Mastro et al. (2019) found that home-range sizes averaged 12.48 km² in West Virginia but can be as large as 27.79 km². Like other species, these home range sizes are dependent on space availability and distribution of resources (Mills and Knowlton 1991). Opportunistic feeding behavior enables this species to consume insects, fruit, amphibians, reptiles, and carrion. In the last 100 years, coyotes have shown dramatic range expansion throughout North America (Hody and Kays 2018). The extirpation of apex predators such as the red wolf has contributed to this expansion by reducing competition for food resources and lowering the risk of predation. Due to their adaptability and social plasticity, coyotes are now one of the dominate predators in the southeast (Mastro et al. 2019).

The Virginia opossum is found throughout central and North America (Walsh and Tucker 2017). Commonly observed as "road kills" throughout Georgia (Boitet and Mead 2014, Ogletree

et al. 2019), the opossum's nomadic behavior has allowed it to adapt to woodland and urban settings. In addition to roadkill observations, its abundance has also been noted by the numbers taken during the trapping season some years ago (Allen et al. 1985). In woodland habitats, it prefers low-lying areas near wetlands and streams. These animals are known to forage extensively for insects, fruit, carrion, and garbage. In Georgia, the average body length is 57 cm with males larger than females. Weight also varies between sex averaging 3.2 kg in males and 2.1 kg in females (Gardner and Sunkuist 2003). In Georgia, home range sizes vary from 0.07 to 0.95 km² (Allen et al. 1985). Walter et al. (2013) found similar home range sizes between 0.10 to 2.0 km² in a Michigan population.

Beavers are a semi-aquatic furbearer with a body length of 74 to 120 cm (Baker and Hill 2003). Adults display a heavily muscled body weighting between 16 and 31.5 kg (Baker and Hill 2003). These herbivores are unique in that they construct dams along small streams in woodland areas to create a desirable habitat. Home-ranges are small, averaging 0.20 km² in size (McClintic et al. 2014). Historically, beavers were heavily harvested as their pelts were in high demand. Current day demand has lessened and most trapping is now nuisance-related as many private landowners do not want to impede the flow of their streams (White et al. 2015).

Similar to beavers in their habitat requirements, the northern river otters and muskrats can be found in flowing streams as well as still water bodies (e.g. ponds, wetlands). Compared to beavers, the river otters are similar in length, but lighter, ranging from 66 to 107 cm in length and 5 to 14 kg in weight. Fish make up over 90.0% of their diet, but otters will also consume crustaceans (Day et al. 2015). Home-range size averages 8.02 km² making them fairly wide-ranging animals (Anderson et al. 2004). Muskrats often live in sympatry with otters, occupying riparian habitats. Body sizes vary from 40 to 70 cm in length with individuals weighing 0.6 to

2.0 kg. Muskrats serve as an important food source for many other animals such as foxes, coyotes, and bobcats.

Studies conducted in the eastern United States have estimated population size, density, abundance, and age ratio among furbearers (Conner et al. 1983, Greene et al. 2016, Kelly and Holub 2008, Martorello et al. 2001, Troyer et al. 2014), but few have been conducted in Georgia. The current study was conducted at the Piedmont National Wildlife Refuge (PNWR), located approximately 25 miles west of Gray, Georgia (Figure 3). The refuge encompasses 14,163 ha of mainly bottomland hardwood and upland pine woodlands (Figure 4). It is divided into 35 compartments, with approximately 400 ha in each one. Before its establishment in 1939, the land had been cleared for agriculture, resulting in a loss of wildlife and massive soil erosion problems (Fish and Wildlife Service 2018). However, through modern management efforts, this area has been restored back to a forest landscape, providing prime habitat for numerous wildlife species. This study was designed to see if the use of trail-cameras was a viable technique to survey furbearer density on the refuge. The objectives were to calculate furbearer density in bottomland and upland habitats and compare paired on-road and off-road density estimates.

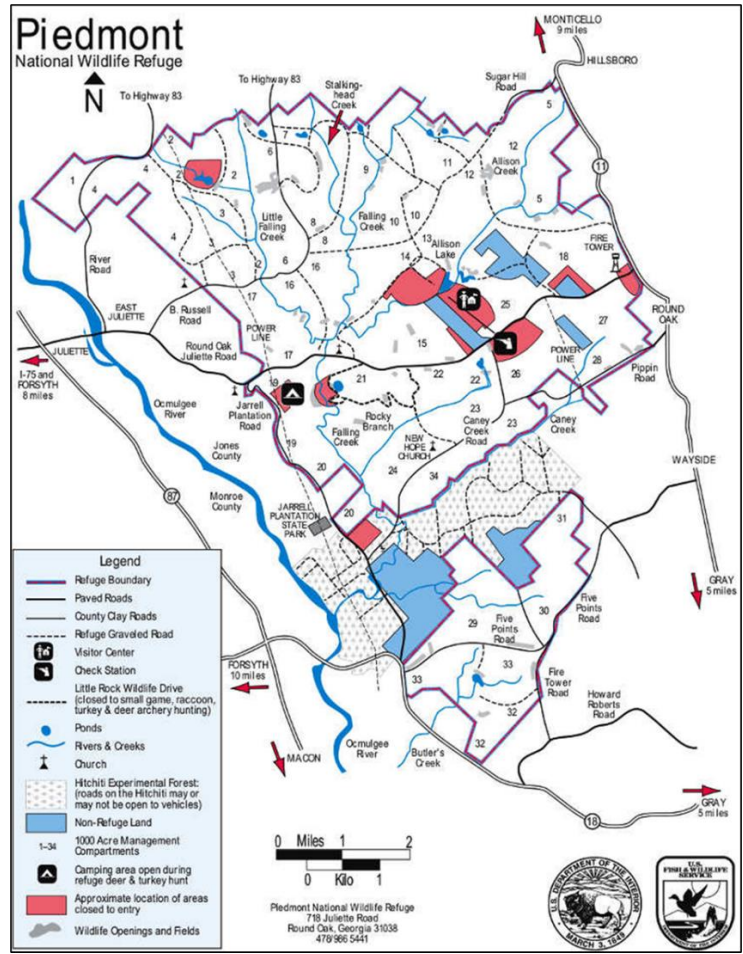


Figure 3: Tearsheet map displaying the Piedmont National Wildlife Refuge (USFW).



Figure 4: Images showing the two major habitats found at the PNWR: (A) upland pine habitat; (B) bottomland hardwood habitat (Images taken by Author).

METHODS

To estimate furbearer density in a portion of the PNWR, 20 BlazeVideo trail-cameras were deployed within compartments eight and fourteen from April 4, 2019 to September 4, 2019. These two compartments lie in the center of the refuge and were chosen due to their isolation from paved roads and other manmade structures (e.g. houses). Camera units were equipped with passive infrared technology and infrared nighttime illuminators for both day and nighttime image captures. Ten camera units were located in hardwood bottomland and ten in upland pine with one camera at each location. Survey stations were established within the study area with cameras positioned 0.4 km apart. This distance is consistent with that used in other population studies (Gerber et al. 2010, Sargeant et al. 1998, Sarmiento et al. 2009). Camera-site locations and elevations were recorded using a Garmin eTrex 20 GPS.

Cameras were monitored every 14 to 21 days to retrieve data, check battery life, adjust cameras that might have moved out of position, and remove any obstructions (i.e. fallen limbs and growing vegetation). Cameras were mounted 50 cm off the ground to obtain optimal images and to ensure smaller animals were adequately detected (Figure 5). To enhance the chance of attracting a furbearer to the area, scent stations were established using bobcat urine (Conner et al. 1983, Symmank et al. 2014). An unused white rag saturated with urine was wrapped around a wooden post 3.04 m directly in front of each camera unit (Figure 6). Images were downloaded in the field to ensure cameras were collecting data properly. Cameras were set on a 1-minute delay period between each image to allow for continuous sampling and to avoid memory card waste from excessive pictures taken during a single contact event. All images were viewed thoroughly in the Georgia College mammalogy lab to determine the species present. Photographs of captured species included date, time of capture, and camera-site location.



Figure 5: Camera unit being mounted in bottomland hardwood habitat (Image taken by Heidi Mead).



Figure 6: Camera unit facing scent post (Image taken by Heidi Mead).

The study was conducted in two phases. During Phase 1 Upland/Bottomland, 10 bottomland and 10 upland camera locations were established to compare density between habitats (Figure 7). Upland camera-sites were located near a forest service road, but not directly on the road. This phase of the study ran the entire length of the trapping period. However, when the Phase 2 Road Comparison began, some cameras were removed. All bottomland cameras and the upland cameras that were not removed (#11,12,13, 18, and 19; Figure 8) continued to collect data during Phase 2. Phase 2 Road Comparison began with the removal of five camera units within the upland habitat. These cameras were redeployed in the same habitat on a forest service road directly adjacent to an already established off-road camera-site (Figure 8). This allowed for the comparison of on-road versus off-road density estimates.

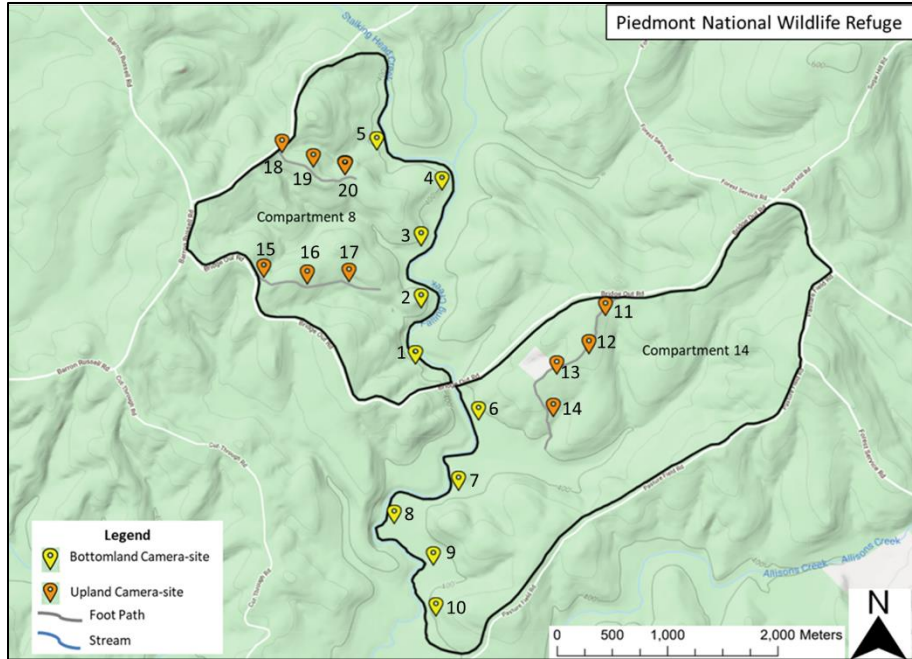


Figure 7: Camera-sites during Phase 1 Upland/Bottomland. An equal number of camera units was present in each habitat type (Map created by author).

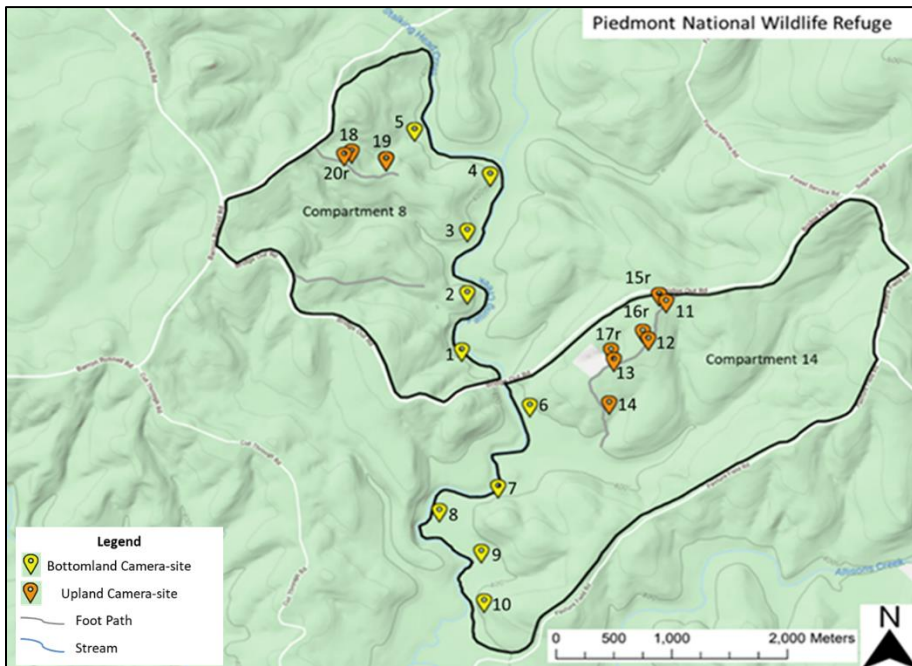


Figure 8: Camera-sites for Phase 2 Road Comparison. Cameras 15, 16, 17 and 20 were removed from their Phase 1 locations and placed directly on the road adjacent to an off-road camera. Camera #14 malfunctioned and was not used this comparison (Map created by author).

A model developed by Rowcliffe et al. (2008) was employed to estimate species density (Equation 1). It was designed to be used for species lacking unique natural markings.

$$D = \frac{y}{t} \frac{\pi}{vr(2+\theta)} \quad (\text{Equation 1})$$

Data collected for each species was applied to this model to determine the number of individuals per km². The t value represents the time of activity in hours; $\frac{y}{t}$ represents the number of photographic captures per unit time; v is species specific distance traveled per trap-day divided by the number of hours active; r is sensor trigger distance; θ is the camera's zone of detection. For nocturnal animals (i.e. opossum, raccoon, bobcat, gray fox) t was set at 11 hours, based on the average nighttime length over the course of the study. The coyote is a cathemeral species so a t of 24 hours was used. Animal movement estimates from studies conducted in the southeast (Table 1) were used to determine the v value. The sensor detection zone θ was found through a series of field trials that measured the detection angle from images obtained by persons walking perpendicular to a mounted camera unit. Marked locations from persons observed on camera allowed for the detection zone to be outlined with surveyor flagging. A Brunton pocket compass was used to measure the delineated detection zone angle which was determined to be 65°. This value correlated well with the detection zone observed in actual camera-site images. Field trials defining trigger distance (r) were also carried out before cameras were deployed in the refuge. This value was determined to be 19.8 m and was calculated through an examination of images collected from camera units mounted behind distance marked objects. This value did not correlate well to trigger distances observed in images taken at the PNWR. Measurements taken at actual camera-sites within the refuge revealed a lower r value. The maximum detection distance in the hardwood bottomland habitat was 7.62 m, whereas in the upland it was 6.09 m.

Table 1: Summary of mean distances traveled by furbearers observed in the southeast.

Species	\bar{x} Distance Traveled/ Trap-day (km)	Location	Reference
Virginia Opossum	1.09	Georgia	Allen et al. 1985
Common Raccoon	1.76	Florida	Walker and Sunquist 1997
Bobcat	2.85	Tennessee	Kitchens and Story 1984
Coyote	8.55	Georgia	Holzman et al. 1992
Gray Fox	4.80	Mississippi	Chamberlain and Leopold 2000

A capture was defined as a solitary furbearer within the camera's field of view (Rowcliffe et al. 2008, Kelly and Holub 2008). If multiple individuals were captured in one image, it was considered multiple captures. For example, if a group of raccoons consisting of a sow and two kits were photographed together, it was considered three captures. However, if animals could not be individually distinguished and were captured within 30 minutes of each other at the same station, it was considered one capture event.

Data was categorized by camera-site and habitat. The number of observations for each species and captures per trap-day at each camera-site were tallied. These values were used to calculate a density estimate and 95% confidence interval using the above model for species at each camera-site. Single factor ANOVA tests were used to compare species density in Upland vs. Bottomland sites in Phase 1, Phase 2 off-road and on-road sites, and estimates between bottomland and upland on-road locations. Additionally, a multiple regression analysis using elevation and habitat data was performed to determine if these variables influenced density.

RESULTS

Using 20 trail-cameras, 3026 trap days were sampled from April 4, 2019 to September 4, 2019. A total of 299 captures of 5 different furbearer species were obtained (Figure 9-10). An additional 94 images collected had unidentifiable probable furbearers and were not included in

the data. Camera #14 malfunctioned after a period of three weeks and was not able to be used for the road comparison.

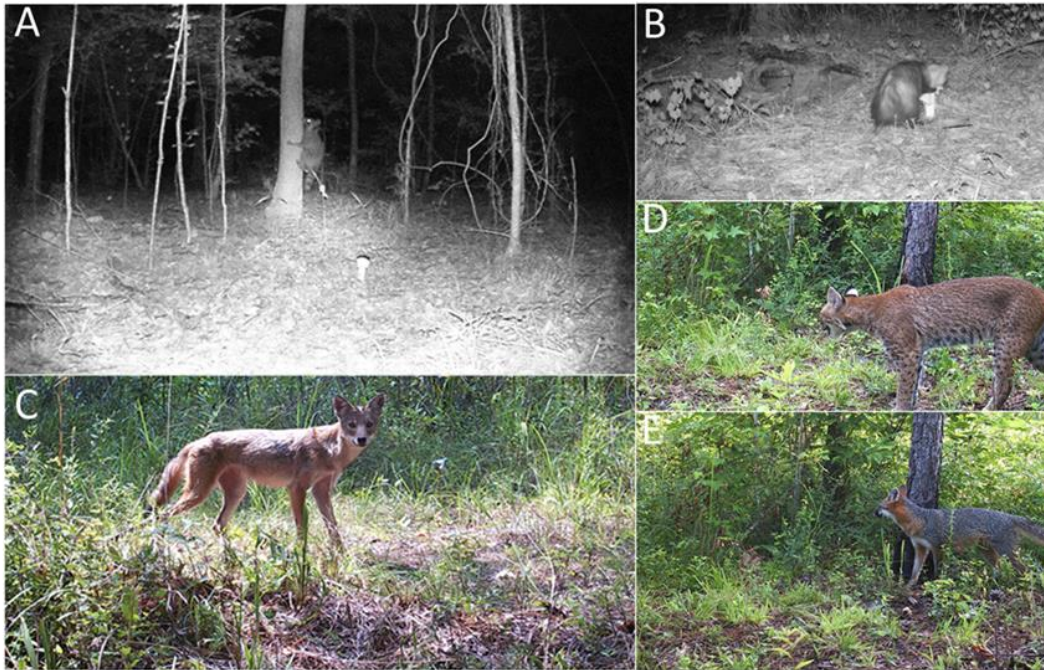


Figure 9: Collection of images showing furbearer species caught on camera: (A) raccoon; (B) Virginia opossum; (C) coyote; (D) bobcat; (E) gray fox.

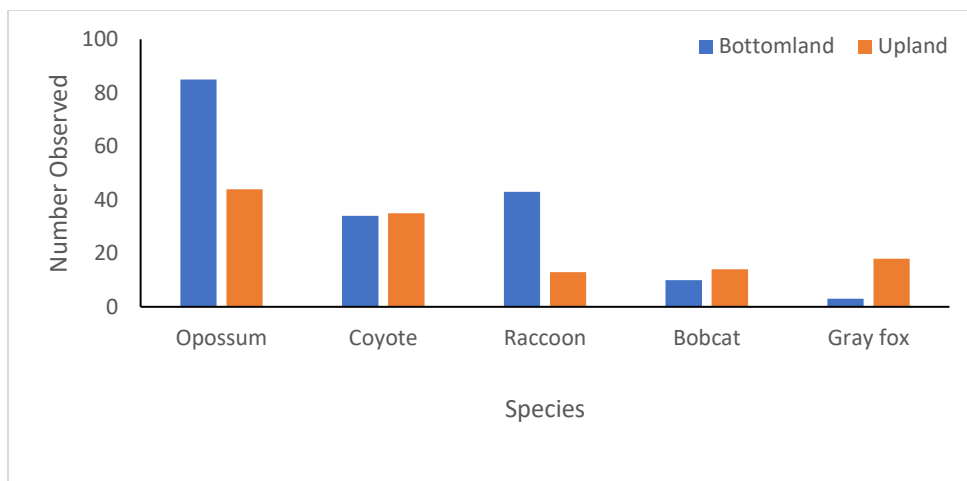


Figure 10: Total number of captures observed for each species.

Virginia opossum

Virginia opossum was the most frequently observed furbearer with 129 captures between both phases. During Phase 1, 107 opossums were detected at 11 of the 20 camera-sites. Of the 9 camera-sites that did not detect opossum, 8 were upland (Appendix 1). All photographs of this

species were recorded during nocturnal or crepuscular periods. Bottomland average density was higher (0.29/km²) than upland (0.18/ km²), but not significantly different ($p= 0.57$, Table 2, Figure 11). The density estimates from combined bottomland and upland habitats was 0.24/km² (Table 4). During the Phase 2 Road Comparison, 22 opossums were recorded from on-road and off-road locations (Appendix 1). Density estimates were higher at off-road locations (0.33/km²) than on-road (0.15/km²), but not found to be significant ($p= 0.62$, Table 2, Figure 12, Appendix 1).

Coyote

A total of 69 coyote captures were recorded during the duration of this study. Forty-six captures were documented during Phase 1. Densities between bottomland and upland habitats were the same at 0.01/km² (Appendix 2). Coyotes were not detected at seven camera-sites during Phase 1, with 2 in the bottomland and 5 in the upland. Combined density estimates for Phase 1 was 0.01/km² (Table 4). Density estimates for the road comparison differed significantly ($p= 0.02$, Table 2, Figure 12). No coyotes were detected at off-road cameras-sites while 23 were observed at on-road sites yielding an estimated density of 0.19/km² (Figure 12, Appendix 2).

Raccoon

There were 56 raccoons captured between both phases, with 53 observed during Phase 1 (Appendix 3). All captures of this species took place during nocturnal or crepuscular hours. Raccoons were detected at 14 of the 20 camera-sites during Phase 1. All camera-sites that did not detect raccoons during this phase were in an upland habitat. Density estimates were higher in bottomland habitat (0.09/ km²) than in upland (0.05/ km²) for Phase 1, but not statistical different ($p=0.32$, Table 2 and Appendix 3). Combined density estimates for Phase 1 was 0.07/km² (Table 4). Only 3 raccoons were detected during the Phase 2 Road Comparison (Appendix 3). Density

estimates between off-road ($0.02/\text{km}^2$) and on-road ($0.01/\text{km}^2$) locations during were also not significantly different ($p = 0.53$, Table 2 and Appendix 3).

Bobcat

Twenty-four bobcats were observed during this study (Appendix 4). Sixteen were documented during Phase 1. During this phase, bobcats were not detected at 4 bottomland and 7 upland stations (Appendix 4). Bobcat estimates for bottomland and upland habitats were comparable at 0.01 bobcats per km^2 (Appendix 4). Combined density estimates for the Phase 1 comparison was $0.01/\text{km}^2$ (Table 4). For the Phase 2 Road Comparison, 1 bobcat was detected at off-road camera-sites and 7 at on-road. Density estimates were higher at on-road locations ($0.05/\text{km}^2$) compared to off-road ($0.003/\text{km}^2$), but not statistically different ($p = 0.14$, Table 2 and Appendix 4).

Gray Fox

Gray fox observations were the lowest among detected species in this study (Appendix 5). Twenty-one capture events were recorded over the trapping duration. During Phase 1, gray foxes were not detected at 15 camera-sites, seven in bottomland habitat and eight in upland. A total of 14 foxes were observed during this phase. Average bottomland density estimates were comparable ($0.02/\text{km}^2$) to upland values ($0.02/\text{km}^2$), and not statistically different ($p=0.86$, Table 2 and Appendix 5). Combined Phase 1 density estimates were $0.02/\text{km}^2$ (Table 4). Estimated densities for the road comparison were not significant ($p=0.35$, Table 2). Gray foxes were not detected at off-road camera-sites whereas on-road camera-sites captured seven individuals ($0.03/\text{km}^2$).

A comparison of bottomland and on-road density estimates revealed no significant differences in density estimates for Virginia opossums, raccoons and gray foxes (Table 2).

Significant differences were observed for bobcats and coyotes ($p=0.04, 0.001$), with roads having higher density estimates (Table 2). A multiple regression analysis revealed raccoon density may be more closely associated with elevation ($p=0.04$) than habitat type (Table 3). Slighter higher density values were observed in areas with lower elevations compared to higher elevation areas. No other species displayed a relationship between elevation and habitat type (Table 3).

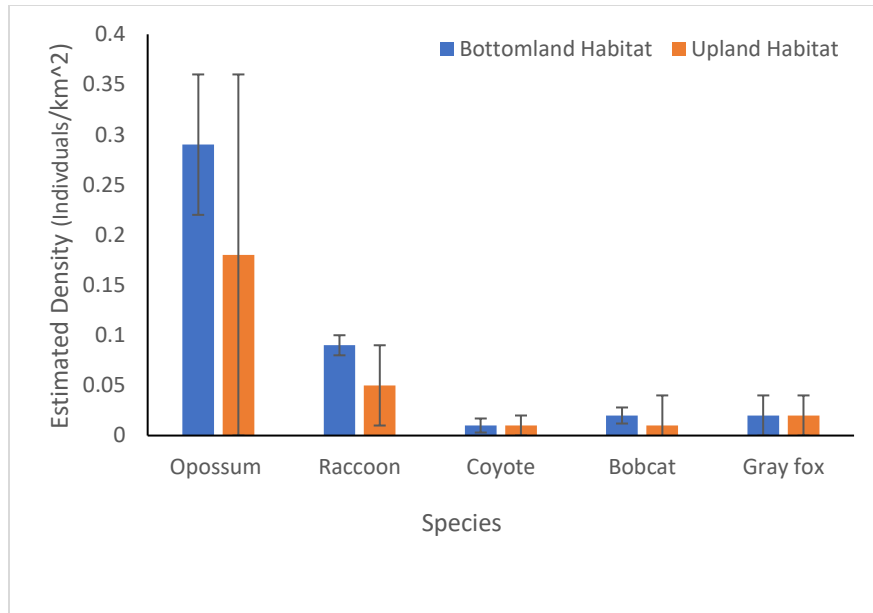


Figure 11: Population density estimates and error bars representing 95% confidence intervals to provide a visual comparison between Phase 1 Bottomland vs Upland by species.

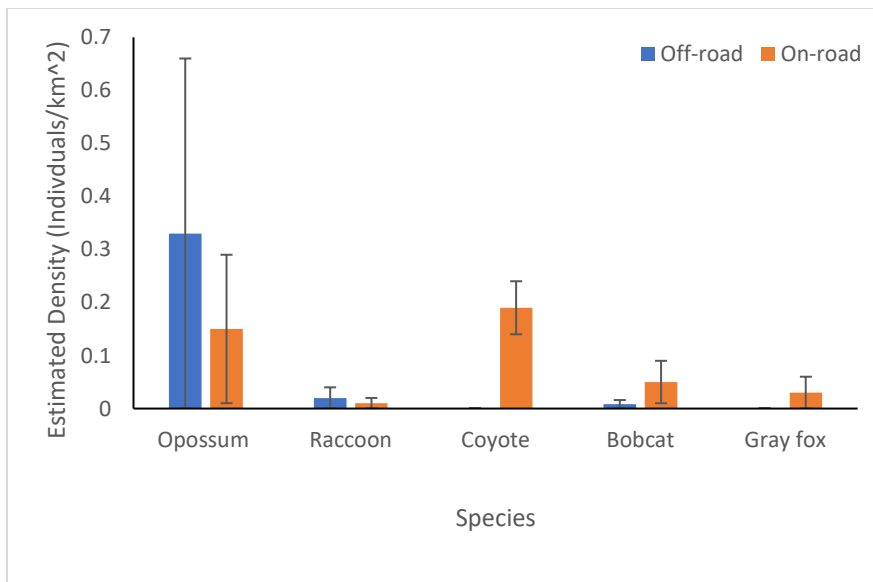


Figure 12: Population density estimates and error bars representing 95% confidence intervals to provide a visual comparison of Phase 2 Off-road vs On-road by species.

Table 2: Average densities \pm 95% CI for Phase 1 Upland/ Bottomland and Phase 2 Road Comparison. *P*-values for Phase 1 Upland/Bottomland indicate no significant difference between bottomland and upland habitats across all species. Phase 2 Road Comparison is insignificant among all species except coyote. Estimates between bottomland and on-road locations were not significant for opossums, raccoons, and gray foxes. Values for coyote and bobcat were found to be significant.

Phase 1 Upland/ Bottomland			
Species	\bar{x} Bottomland/ km²	\bar{x} Upland/ km²	p-value
Virginia Opossum	0.29 \pm 0.07	0.18 \pm 0.18	0.57
Raccoon	0.09 \pm 0.01	0.05 \pm 0.04	0.32
Bobcat	0.02 \pm 0.008	0.01 \pm 0.03	0.81
Coyote	0.01 \pm 0.007	0.01 \pm 0.01	0.79
Gray Fox	0.02 \pm 0.04	0.02 \pm 0.03	0.86
Phase 2 Road Comparison			
Species	\bar{x} Off-Road/ km²	\bar{x} On-road/km²	p-value
Virginia Opossum	0.33 \pm 0.33	0.15 \pm 0.14	0.62
Raccoon	0.02 \pm 0.03	0.01 \pm 0.04	0.53
Bobcat	0.008 \pm 0.02	0.05 \pm 0.04	0.14
Coyote	0	0.19 \pm 0.05	0.02
Gray Fox	0	0.03 \pm 0.05	0.35
Bottomland vs Road ANOVA			
Species	\bar{x} Bottomland/ km²	\bar{x} On-road/ km²	p-value
Virginia Opossum	0.29 \pm 0.07	0.15 \pm 0.14	0.89
Raccoon	0.09 \pm 0.01	0.01 \pm 0.04	0.13
Bobcat	0.02 \pm 0.04	0.05 \pm 0.04	0.04
Coyote	0.01 \pm 0.007	0.19 \pm 0.05	0.001
Gray Fox	0.02 \pm 0.04	0.03 \pm 0.05	0.15

Table 3: Values obtained through a multiple regression analysis comparing habitat type and elevation. Raccoons were the only species that displayed a significant difference ($p < 0.05$)* between elevation and habitat type, with higher densities observed at lower elevation in camera-sites.

Species	Combined Models		Elevation Model		Habitat Model	
	f-value	p-value	f-value	p-value	f-value	p-value
Opossum	0.58	0.57	1.03	0.32	0.31	0.58
Raccoon	3.01	0.07	4.74	0.04*	1.03	0.32
Bobcat	0.42	0.65	0.45	0.50	0.02	0.87
Coyote	1.57	0.23	0.66	0.42	0.05	0.82
Gray Fox	0.31	0.73	0.10	0.74	0.02	0.86

Table 4: Combined density values for upland and bottomland habitats.

Species	\bar{x} Upland and Bottomland Density Combined
Virginia opossum	0.24 \pm 0.17
Raccoon	0.07 \pm 0.01
Coyote	0.01 \pm 0.008
Bobcat	0.01 \pm 0.01
Gray fox	0.02 \pm 0.02

DISCUSSION

Density estimates for opossums and gray foxes were nonsignificant between upland and bottomland habitats, and between bottomland and on-road locations. Wildlife officials seeking to estimate densities for these two species should consider placing cameras at on-road locations in either habitat type. On-road camera placement is less labor intensive and will produce density estimates indicative of other habitats. For raccoons, a multiple regression analysis indicated elevation may influence density more than habitat type. Cameras surveying raccoon populations should be located at different elevations along roads to ensure a representative sample is obtained. For coyotes, no significant difference in density estimates between bottomland and upland habitats was present. However, density estimates were significantly different between on- and off-road locations in upland habitat, and between bottomland and on-road locations. Cameras located directly on roads produced higher capture rates than off-road sites, resulting in density estimates that were likely inflated. Surveys targeting coyotes should employ cameras at off-road locations to ensure a more representative density estimate. Bobcat density differed significantly between bottomland habitat and on-road upland locations. Surveys targeting bobcats should consider placing cameras at off-road locations in either bottomland or upland habitat. For general species monitoring, on-road locations for all species would be sufficient.

Camera traps allowed for the monitoring of furbearing species at the PNWR and were found to be fairly well-suited for gathering large amounts of data over an extended period of time, however, the nighttime photographic performance was a major issue we dealt with during the entire study. Images taken of nocturnal animals were often blurred or obscured by the high intensity IR flash. A total of 94 images taken during nighttime hours were unidentifiable. This undoubtedly lowered the density estimates obtained. If the 94 unidentifiable images were

distributed proportionally by the total number of captures, the revised density estimates for Phase 1 would have been higher. Opossums would have had a revised combined density of 0.31/km², raccoons 0.11/km², coyotes 0.02/km², bobcats 0.02/km², and gray foxes 0.05/km². Some of these revised estimates are noticeably higher. Ensuring that cameras take quality nighttime photographs is critical in obtaining more accurate density estimates. Cameras should be equipped with an IR flash that is not overly bright at close distances, but still bright enough to adequately illuminate animals at longer distances. In addition to the high intensity IR flashes, thousands of false triggers were recorded by each camera unit at the beginning of the study. Some cameras recorded over 2000 unusable images a week. To prevent this, detection settings were adjusted to make the cameras less sensitive. Wildlife managers should be familiar with the sensitivity of cameras being used as overly sensitive units will exhaust battery sets and use up memory storage.

Overall camera performance excluding nighttime image quality was sufficient, but extremely labor intensive in terms of deployment and monitoring. Since no roads paralleled hardwood bottoms in the study area, off-trail hiking was necessary to establish camera-sites. Upland camera placement required less labor but was still walking intensive. When checking all 20 cameras alone, one could expect to walk approximately 13 miles. Data collection took place unattended, but regular visits every 14 to 21 days were needed to change memory cards, remove vegetation blocking camera view, and ensure cameras were still functioning properly.

The results of this study show that placing cameras directly on roads will provide accurate density estimates for opossums, raccoons, and gray foxes. Cameras used to collect population data on coyotes and bobcats will require off-road camera placement. The initial camera placement design is an aspect that varies considerably between studies and should be

considered when surveying furbearers. Cameras can be systematically spaced (such as the ones in this study), randomly placed, placed at features associated with wildlife activity, or placed at areas with known wildlife sightings. Even though it is well known that randomization-based designs allow for the greatest reliability and validity of statistical estimates, many camera surveys do not use this approach. Sollmann et al. (2013) found that such methods can have negative consequences on the reliability and applicability of the data collected. Population studies of medium to large sized carnivore species should be aware of road usage as it has been documented that these animals frequently use roads and other travel routes constructed by humans (Sollmann et al. 2013, Mann et al. 2015). Kolowski and Forrester (2017) demonstrated bias associated with trail-camera placement, finding that cameras placed at logs and along game trails had significantly higher capture rates than cameras placed at nearby random locations. The camera locations in this study were not random, but the Phase 2 Road Comparison revealed capture rates tended to be higher at on-road locations than nearby off-road locations, especially for coyotes and bobcats.

Some researchers are reluctant to use a random placement method due to lower capture rates and instead include an equal mixture of cameras placed at on-trail and off-trail locations. Kolowski and Forrester (2017) acknowledged this method, claiming it may mitigate the possibility of inflated capture rates, but its consequences are still unknown. However, Mann et al. (2015) found that employing a mixed design of cameras on- and off-roads does provide a more reliable estimation in detection probability. Larrucea et al. (2007) found adult coyotes were photographed more frequently on roads and near urban areas whereas juveniles were more often photographed away from these areas. As seen in this study, carnivores were more likely to be detected on roads, whereas omnivores seemed to be indifferent of roads.

The implications of other published studies reveal camera-traps do not always provide an unbiased sample. Species detection is not equal over space and time and it is recommended that studies using trail-cameras consider employing a design that places cameras on and off roads in order to achieve a more representative sample (Mann et al. 2015). Although some form of random sampling is recommended in most scenarios, studies that aim to maximize capture of a certain species can target specific habitat features (i.e. roads, game trails, or water features) (Kolowski and Forrester 2017).

An additional issue regarding the validity of a camera survey is the number of cameras deployed at each site. Pease et al. (2016) surveyed wildlife in southern Illinois deploying up to four cameras at each camera-site. The authors found a 64% increase in mean detections between one and two cameras per camera-site, and 63% increase from two to four cameras per site. More cameras per site generally lead to an overall increase in the number of species detected. However, this is often not feasible as survey designs may be logistically constrained.

Some species (e.g. gray fox, bobcat) had low capture rates throughout the study. This brings into question the accuracy of obtained density values as it is unclear if an adequate number of photographs is needed to produce statistically reliable results. Species in which lower detection rates occurred (e.g. gray fox) may need to be monitored for longer periods of time to ensure an accurate assessment of the population is taking place.

The density estimates in this study are lower than other published estimates. The model used in this study was designed for species that are not uniquely identifiable, but there are numerous factors that can influence the density estimates. Using Virginia opossums as an example, the combined density value for Phase 1 Bottomland/Upland was $0.24/\text{km}^2$. Changing the v from the original 1.09 km to 0.56 km, the lowest daily movement distance recorded by

Allen et al. (1985), would result in a density of $0.46/\text{km}^2$, almost twice the original value. The zone of detection θ and sensor trigger distance r can also influence estimates as lower values increase the generated density estimate. Camera parameters vary to some degree between units and may be sensitive to animal size (Swann et al. 2004). Field trials should be conducted to verify the accuracy of the unit being employed. The species-specific distance traveled per day v is more problematic. Ideally, this value should be estimated at the same time and place as the camera survey (Rowcliffe et al. 2008). Like this study, it is often not feasible and estimates from other movement studies in the same region are employed. Rowcliffe et al. (2008) noted using movement estimates from other studies likely introduces a degree of bias as movement distances will vary by location, even in the same region. These density estimates should be interpreted cautiously and used as rough approximations.

Phase 1 density estimates ($0.24\text{-}0.31/\text{km}^2$, combined and revised) for Virginia opossums in this study were lower than other published estimates. Weckerly and Kennedy (1987) estimated 0.9 to 8.4 opossums/ km^2 in Tennessee through live-trapping methods. Stout and Sonenshine (1974) estimated $5.0/\text{km}^2$ in Virginia using mark-recapture. Gehrt et al. (1997) found $3.79/\text{km}^2$ in a southern Texas population through live-trapping methods. Conner et al. (1983) estimated a population in Kansas to be $10.1/\text{km}^2$ using track counts. Population densities in Georgia are currently unknown, but thought to be high, especially in urban areas (Georgia Wildlife Resources Division 2006). The Phase 2 Road comparison revealed no statistical difference between off-road and on-road camera locations. Mann et al. (2015) found omnivores are indifferent to roads, traveling them less frequently than carnivores. A bottomland road system did not exist in the study area so it is unknown if a higher road density would exist in this habitat compared to roads in the upland habitat. Opossum density was estimated to be higher in

bottomland areas than upland, but not significantly. In the bottomland habitat, cameras #6 and #7 had noticeably more captures compared to others. These cameras were in locations that lacked dense understory vegetation, possibly resulting in more frequent use. Camera #13 had many more captures than other upland cameras in the study. It was located in a transitional habitat that lead to a small stream, possibly attracting more individuals to the area.

Average raccoon density was slightly higher in bottomland habitat than in upland but was not found to be significant. However, as indicated in the multiple regression analysis, elevation may be a better indicator of density than habitat type, with higher densities observed at lower elevation areas. The Phase 1 density estimates (0.07-0.11/km², combined and revised) in this study were lower than other studies. Typical densities in rural areas in the southeast U.S. range from 1.0 to 27/km² (Moore and Kennedy 1985). Kennedy et al. (1986) found an average of 5.0/km² in a Tennessee population using mark-recapture methods. A population in the Florida Keys was estimated to have 3.9/km² using a similar method (Bigler et al. 1981). A thorough literature review did not find any studies related to raccoon population density in Georgia. Gehrt (2003) found that caution should be taken when comparing studies of raccoons as populations can fluctuate rapidly from year to year. For the road comparison, the off-road density estimate was higher than on-road, but not statistically different. Similar to what was observed for opossums, roads are less frequented by omnivores (Mann et al. 2015).

Bobcat density was estimated to be slightly higher in bottomland than upland habitats for Phase 1. The calculated density (0.01-0.02/km², combined and revised) is lower than other studies. Baker et al. (2001) estimated a density of 0.54/km² using observational and scat collection data in population located on Cumberland Island, Georgia. Wassmer et al. (1988) reported a density of 0.14 to 0.42/km² using live-trapping methods in south-central Florida.

Heilbrun et al. (2006) found a density of $0.48/\text{km}^2$ in central Texas using trail-cameras. Knick (1990) estimated a bobcat density of $0.08/\text{km}^2$ from harvest data in southeastern Idaho. In the current study, data collected for the road comparison was nonsignificant, but density estimates at on-road ($0.05/\text{km}^2$) locations were slightly higher than off-road ($0.008/\text{km}^2$) locations. As previously noted, Mann et al. (2015) found road usage by carnivores to be higher compared to omnivores and insectivores. Anderson and Lovallo (2003) noted difficulty in obtaining accurate bobcat population estimates as this species is widely dispersed, occurring at low densities across the landscape. Bobcats prefer deciduous woodlands, but are considered habitat generalist, as they can transition their movement between vegetative types, especially in regard to prey density (Litvaitis et al. 1986).

The estimated density for coyotes was equal for both habitat types in Phase 1. Captures were similar between cameras, except for camera #4, which recorded many more coyotes. This camera was in an open area near a small game trail, making for the possibility some individuals were captured multiple times traveling back and forth along the trail. Holzman et al. (1992) found that coyotes did not select for specific habitats during daylight hours but did preferred young pine plantations during the night. Phase 1 density estimates ($0.01\text{-}0.02/\text{km}^2$, combined and revised) were lower compared to other studies. Babb and Kennedy (1989) recorded a coyote density of $0.35/\text{km}^2$ in Tennessee using live-trapping methods. Henke and Bryant (1999) found a density range of $0.12\text{ to }0.14/\text{km}^2$ using harvest data from a Texas population. Larrucea et al. (2007) estimated a population to be $1.63/\text{km}^2$ using trail-cameras in California. All capture events for the Phase 2 Road Comparison took place at on-road locations, suggesting roads are more often used. Larrucea et al. (2007) also found that coyotes were more likely to be captured at on-road camera-sites versus off-road locations.

Estimated density for gray foxes in the bottomland habitat and upland habitat were similar. Multiple camera-site locations in both habitats did not record the presence of any gray foxes during Phase 1. Captures recorded at on-road locations were higher, although only 3 captures in total were documented. Density estimates (0.02-0.05/km², combined and revised) in this study were lower than others. Lord (1961) found a density of 0.86/km² in Florida using live-trapping methods. An additional study by Grinnell et al. (1937) estimated density at 0.4/km² using harvest data from a California population.

Although density values for Phase 1 were nonsignificant across species, many of the cameras located in upland habitat had zero captures whereas most cameras in the bottomland habitat captured all species at least once. This is possibly due to habitat selection and travel movement. Bottomland areas in compartment 8 and 14 have a relatively clear understory, allowing for easier travel, especially along stream beds. These areas also correlate to the preferred habitat of many species as previously mentioned. The lower frequency of detections at upland locations can likely be attributed to the thick understory layer. Traveling in these areas would be difficult, even for smaller animals as the vegetation is dense. Compartments in the PNWR are on a 2 to 3-year burn rotation. The compartments chosen for this study have not been recently burned so it is unclear if sightings would be more frequent in upland areas that have a more sparsely distributed understory layer.

The model used in this study allowed for the density estimation of five furbearer species lacking individually recognizable markings. As trail-camera surveys become more popular, it is likely that further refinement of this method will improve its applicability. A major disadvantage in the employment of this model is the need for accurate daily movement values. Density estimates obtained from movement values in other studies should be interpreted cautiously.

Estimating furbearer populations with trail-cameras has far-reaching management implications in that these animals can be monitored without the need for physical capture or handling. This will likely allow managers to obtain larger data sets than typically gathered in physical capture studies, especially in regard to species that are elusive.

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Appendix 1: The number of trap days (TD), number of Virginia opossums, captures per TD, and density estimates at each camera station in A) bottomland and Upland habitat and B) road and off-road camera sites. Average density estimates are accompanied by a \pm 95% confidence interval. Lower half of table displays population data for the road comparison phase. For B), camera stations in the same row were paired, with one directly adjacent to the other (e.g. Station #11 paired with station #15rd).

A. Phase 1: Upland vs. Bottomland							
Opossum Bottomland				Opossum Upland			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
1 (160)	4	0.025	0.14	11 (143)	0	0	0
2 (160)	11	0.068	0.38	12 (160)	0	0	0
3 (143)	1	0.006	0.03	13 (160)	32	0.20	1.41
4 (160)	3	0.018	0.10	14 (24)	0	0	0
5 (160)	7	0.043	0.24	15 (60)	0	0	0
6 (160)	26	0.162	0.91	16 (81)	0	0	0
7 (160)	27	0.168	0.94	17 (81)	5	0.06	0.43
8 (160)	0	0	0	18 (160)	0	0	0
9 (160)	2	0.012	0.06	19 (160)	0	0	0
10 (160)	4	0.025	0.14	20 (81)	0	0	0
$\bar{x} \pm 95\%$ CI		0.05	0.29 ± 0.07	$\bar{x} \pm 95\%$ CI		0.02	0.18 ± 0.18
B. Phase 2: Road Comparison							
Off-Road Captures				On-Road Captures			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
11 (62)	0	0	0	15rd (79)	1	0.012	0.08
12 (79)	0	0	0	16rd (79)	1	0.012	0.08
13 (79)	15	0.189	1.33	17rd (79)	0	0	0
18 (79)	0	0	0	20rd (79)	5	0.063	0.4
$\bar{x} \pm 95\%$ CI		0.04	0.33 ± 0.33	$\bar{x} \pm 95\%$ CI		0.02	0.15 ± 0.14

Appendix 2: The number of trap days (TD), number of coyotes, captures per TD, and density estimates at each camera station in A) bottomland and Upland habitat and B) road and off-road camera sites. Average density estimates are accompanied by a \pm 95% confidence interval. Lower half of table displays population data for the road comparison phase. For B), camera stations in the same row were paired, with one directly adjacent to the other (e.g. Station #11 paired with station #15rd).

A. Phase 1: Upland vs. Bottomland							
Coyote Bottomland				Coyote Upland			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
1 (160)	3	0.01	0.01	11 (143)	2	0.02	0.02
2 (160)	1	0.006	0.004	12 (160)	0	0	0
3 (143)	2	0.01	0.01	13 (160)	0	0	0
4 (160)	16	0.1	0.07	14 (24)	0	0	0
5 (160)	3	0.01	0.01	15 (60)	0	0	0
6 (160)	0	0	0	16 (81)	1	0.01	0.01
7 (160)	0	0	0	17 (81)	0	0	0
8 (160)	2	0.01	0.008	18 (160)	1	0.01	0.01
9 (160)	2	0.01	0.008	19 (160)	2	0.02	0.02
10 (160)	5	0.03	0.02	20 (81)	6	0.07	0.06
$\bar{x} \pm 95\%$ CI		0.02	0.01 ± 0.007	$\bar{x} \pm 95\%$ CI		0.01	0.01 ± 0.01
B. Phase 2: Road Comparison							
Off-Road Captures				On-Road Captures			
Station (TD)	Number Observed	Captures (#/TD)	Density/(km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
11 (62)	0	0	0	15rd (79)	6	0.07	0.20
12 (79)	0	0	0	16rd (79)	8	0.10	0.27
13 (79)	0	0	0	17rd (79)	0	0	0
18 (79)	0	0	0	20rd (79)	9	0.11	0.30
$\bar{x} \pm 95\%$ CI		0	0	$\bar{x} \pm 95\%$ CI		0.07	0.19 ± 0.05

Appendix 3: The number of trap days (TD), number of raccoons, captures per TD, and density estimates at each camera station in A) bottomland and Upland habitat and B) road and off-road camera sites. Average density estimates are accompanied by a \pm 95% confidence interval. Lower half of table displays population data for the road comparison phase. For B), camera stations in the same row were paired, with one directly adjacent to the other (e.g. Station #11 paired with station #15rd).

A. Phase 1: Upland vs. Bottomland							
Raccoon Bottomland				Raccoon Upland			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
1 (160)	2	0.01	0.04	11 (143)	0	0	0
2 (160)	0	0	0	12 (160)	2	0.01	0.05
3 (143)	1	0.006	0.02	13 (160)	1	0.006	0.02
4 (160)	3	0.01	0.06	14 (24)	0	0	0
5 (160)	1	0.006	0.02	15 (60)	0	0	0
6 (160)	8	0.05	0.17	16 (81)	4	0.04	0.21
7 (160)	5	0.03	0.10	17 (81)	3	0.03	0.16
8 (160)	15	0.09	0.32	18 (160)	0	0	0
9 (160)	2	0.01	0.04	19 (160)	2	0.02	0.10
10 (160)	6	0.03	0.13	20 (81)	0	0	0
$\bar{x} \pm 95\%$ CI		0.02	0.09 \pm 0.02	$\bar{x} \pm 95\%$ CI		0.01	0.05 \pm 0.04
B. Phase 2: Road Comparison							
Off-Road Captures				On-Road Captures			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
11 (62)	0	0	0	15rd (79)	1	0.01	0.05
12 (79)	1	0.01	0.05	16rd (79)	0	0	0
13 (79)	1	0.01	0.05	17rd (79)	0	0	0
18 (79)	0	0	0	20rd (79)	0	0	0
$\bar{x} \pm 95\%$ CI		0.006	0.02 \pm 0.03	$\bar{x} \pm 95\%$ CI		0.003	0.01 \pm 0.04

Appendix 4: The number of trap days (TD), number of bobcats, captures per TD, and density estimates at each camera station in A) bottomland and Upland habitat and B) road and off-road camera sites. Average density estimates are accompanied by a \pm 95% confidence interval. Lower half of table displays population data for the road comparison phase. For B), camera stations in the same row were paired, with one directly adjacent to the other (e.g. Station #11 paired with station #15rd).

A. Phase 1: Upland vs. Bottomland							
Bobcat Bottomland				Bobcat Upland			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
1 (160)	0	0	0	11 (143)	0	0	0
2 (160)	0	0	0	12 (160)	1	0.006	0.01
3 (143)	1	0.01	0.02	13 (160)	2	0.02	0.06
4 (160)	3	0.03	0.07	14 (24)	0	0	0
5 (160)	1	0.01	0.02	15 (60)	0	0	0
6 (160)	2	0.02	0.05	16 (81)	0	0	0
7 (160)	0	0	0	17 (81)	0	0	0
8 (160)	1	0.01	0.02	18 (160)	0	0	0
9 (160)	2	0.02	0.053	19 (160)	0	0	0
10 (160)	0	0	0	20 (81)	3	0.03	0.09
$\bar{x} \pm 95\%$ CI		0.01	0.02 \pm 0.008	$\bar{x} \pm 95\%$ CI		0.006	0.01 \pm 0.03
B. Phase 2: Road Comparison							
Off-Road Captures				On-Road Captures			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
11 (62)	0	0	0	15rd (79)	4	0.05	0.13
12 (79)	1	0.012	0.03	16rd (79)	1	0.012	0.03
13 (79)	0	0	0	17rd (79)	0	0	0
18 (79)	0	0	0	20rd (79)	2	0.025	0.06
$\bar{x} \pm 95\%$ CI		0.003	0.008 \pm 0.02	$\bar{x} \pm 95\%$ CI		0.02	0.05 \pm 0.04

Appendix 5: The number of trap days (TD), number of gray foxes, captures per TD, and density estimates at each camera station in A) bottomland and Upland habitat and B) road and off-road camera sites. Average density estimates are accompanied by a \pm 95% confidence interval. Lower half of table displays population data for the road comparison phase. For B), camera stations in the same row were paired, with one directly adjacent to the other (e.g. Station #11 paired with station #15rd).

A. Phase 1: Upland vs. Bottomland							
Gray fox Bottomland				Gray fox Upland			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
1 (160)	0	0	0	11 (143)	0	0	0
2 (160)	0	0	0	12 (160)	0	0	0
3 (143)	0	0	0	13 (160)	0	0	0
4 (160)	1	0.006	0.08	14 (24)	0	0	0
5 (160)	0	0	0	15 (60)	1	0.01	0.02
6 (160)	0	0	0	16 (81)	0	0	0
7 (160)	0	0	0	17 (81)	0	0	0
8 (160)	1	0.006	0.08	18 (160)	0	0	0
9 (160)	0	0	0	19 (160)	0	0	0
10 (160)	1	0.006	0.08	20 (81)	10	0.12	0.19
$\bar{x} \pm 95\%$ CI		0.001	0.02 ± 0.04	\bar{x}		0.01	0.02 ± 0.03
B. Phase 2: Road Comparison							
Off-Road Captures				On-Road Captures			
Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)	Station (TD)	Number Observed	Captures (#/TD)	Density (#/km ²)
11 (62)	0	0	0	15rd (79)	0	0	0
12 (79)	0	0	0	16rd (79)	0	0	0
13 (79)	0	0	0	17rd (79)	0	0	0
18 (79)	0	0	0	20rd (79)	7	0.08	0.14
$\bar{x} \pm 95\%$ CI		0	0	\bar{x}		0.02	0.03 ± 0.05