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Mesopredator Distribution, Abundance and Potential Competition with the American Burying Beetle (Nicrophorus Americanus) at Fort Chaffee Joint Maneuver Training Center

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MESOPREDATOR DISTRIBUTION, ABUNDANCE AND POTENTIAL COMPETITION WITH THE AMERICAN BURYING BEETLE (*NICROPHORUS AMERICANUS*) AT FORT CHAFFEE JOINT MANEUVER TRAINING CENTER

By

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THESIS ABSTRACT

The American burying beetle (*Nicrophorus americanus*, hereafter ABB) was listed as an endangered species in 1989 and many hypotheses have been developed to explain their range-wide decline. I investigated the carcass competition hypothesis that implicates increased competition between vertebrate scavengers and ABBs for appropriate-sized carcasses as a cause for ABB decline. Predators of medium size that occupy an intermediate trophic level (hereafter mesopredators) are potential competitors for carcasses. I used camera trapping to assess mesopredator abundances in nine different habitats at Fort Chaffee Joint Maneuver Training Center (FCJMTC) in western Arkansas because this area supports the largest known population of ABBs in the state. In part one of the study, I examined mesopredator presence at random locations over two field seasons and captured photos of Virginia opossum, northern raccoon, coyote and bobcat activity over 2,076 trap nights. Coyotes were the most captured mesopredator at 60 independent sightings followed by northern raccoons (37 sightings), bobcats (12 sightings) and Virginia opossums (11 sightings). A random encounter model was used to obtain mesopredator density estimates and identify potential correlations between mesopredator and ABB abundances. Density estimates were highest for mesopredators in the bottomland hardwood and deciduous habitats while ABBs are most abundant in grassland/ prairie and oak habitats. A negative relationship was seen between mesopredator counts per 100 trap nights and distance to the edge of the base (estimate = -0.0006, SE = 0.0002, p= 0.003) whereas ABBs are found in the central area of the base. In part two of the study, I examined mesopredator presence at sites in conjunction with yearly ABB trapping efforts. I captured 117 independent animal sightings at 72 sites over two seasons and 216 trap nights. Commonly captured mesopredators included Virginia opossums, northern raccoons, coyotes and bobcats, which made up 55% of all animal sightings.

Virginia opossums were the most captured mesopredator at 48 independent sightings followed by northern raccoons, coyotes and bobcats at 9, 4 and 3 independent sightings respectively. A high ABB capture zone was determined from the ABB census data and a Wilcoxon Rank Sum test was conducted between sites inside and outside the high ABB zone and mesopredators per trap day counts. When the seasons were combined there were significantly more mesopredator captures outside of the ABB areas compared to within the high ABB areas (W=409, P<0.01) providing evidence of potential competition especially between ABBs and Virginia opossums. A negative relationship was found between ABB and mesopredator counts (estimate = -0.34, SE = 0.14, p<0.05) when compared by site. American burying beetles may have avoided locations that had high mesopredator numbers. Management for ABBs should minimize attractiveness to mesopredators, especially Virginia opossums, by limiting edge habitats as well as wooded and densely overgrown areas.

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THESIS INTRODUCTION

American Burying Beetle Decline

After American burying beetles (*Nicrophorus americanus*, hereafter ABB) were listed as an endangered species, research increased rapidly and numerous hypotheses were proposed to explain their decline. Sikes and Raithel (2002) stated that a combination of causes most likely explained the range-wide decline of the species. Suggested hypotheses for the ABB decline range from DDT and pesticide use to artificial lighting attracting beetles and habitat loss (Sikes and Raithel 2002). Many of these hypotheses have been rejected as the primary explanation for the ABB decline. For example, while DDT and pesticides can eliminate *Nicrophorus spp.* populations (Hoffmann et al. 1949) pesticide use does not explain the pattern in ABB disappearance. Populations remain in areas where pesticides were widely used while populations in areas not exposed to pesticides were lost. In fact, most ABB populations disappeared 25 years before DDT was widely used (Kozol 1995, Raithel 1991). Furthermore, ABBs are not frequently attracted to artificial light (Anderson and Peck 1985) and populations have been found in areas that have abundant artificial lighting making this hypothesis an unlikely cause of the decline (Sikes and Raithel 2002). While early researchers hypothesized that the decline occurred because of habitat loss due to ABBs presumed reliance on old growth forests (Anderson 1982), subsequent research has found that ABBs are in fact vegetation generalists (Lomolino et al. 1995). Research has shown that ABBs can be captured in different habitat types as long as the habitat contains sufficient carrion resources (Lomolino and Creighton 1996).

Three hypotheses for the decline and subsequent endangerment of ABB considered most plausible are: (1) increased congener competition for carcasses, (2) decline of suitable carrion resources and (3) increased competition between vertebrate scavengers and ABBs (Sikes and

Raithel 2002). According to the United States Fish and Wildlife Service (USFWS) ABB recovery plan, these three hypotheses are widely accepted although much of the evidence for them is circumstantial and further research is necessary (USFWS 2015). The increase in congener competition hypothesis aligns with the subsequent two hypotheses because congener competition is expected to increase if carrion availability decreases. *Nicrophorus orbicollis*, a congener of *N. americanus*, is most similar to ABB in regards to historic range and tolerances. In trapping studies, *N. orbicollis* has been found to be nearly ten times more abundant than ABB (Lomolino and Creighton 1996, Amaral et al. 1997).

The vertebrate competition hypothesis implicates habitat fragmentation as an indirect cause for the ABB decline due to increased densities of vertebrate scavengers in fragmented habitats. Included in the list of likely competitors for carrion are red fox (*Vulpes vulpes*), northern raccoon (*Procyon lotor*), Norway rat (*Rattus norvegicus*), feral cat (*Felis catus*), Virginia opossum (*Didelphis virginiana*), coyote (*Canis latrans*), American crow (*Corvus brachyrhynchos*) and striped skunk (*Mephitis mephitis*) (Sikes and Raithel 2002). In addition, the loss of ideal carrion hypothesis is a further refinement of the previous hypothesis that explains that some potential carrion species of ideal size for ABB use (80-100g) have gone extinct or declined including the passenger pigeon (*Ectopistes migratorius*) and northern bobwhite (*Colinus virginianus*) (Guthery et al. 2000). Evidence relating ABB abundance to the available carrion has been limited at best and there has been little documentation of vertebrate competition for carrion resources in areas where ABB occur, nevertheless these hypotheses have been frequently referenced in the literature.

American Burying Beetle

The ABB, once prevalent throughout the eastern part of North America has now declined by nearly 90% in numbers and range (Bedick 1999). In 1989, the USFWS placed the American burying beetle, the largest member of the Silphidae family in North America, on the endangered species list (Creighton 2009). *Nicrophorus americanus*, like other members of the genus *Nicrophorus*, is a carrion specialist and requires small animal carcasses for successful reproduction. ABBs use their olfactory senses to find carcasses and then attract a mate. The pair works together to strip and treat the carcass with oral and anal secretions to reduce bacterial growth. They bury the carrion and lay eggs on or near the carcass and the carcass provides a safe environment and nourishment for the offspring (Walker 2007). Beetles are active from late April through September when nighttime temperatures exceed 15 °C. While members of the *Nicrophorus* genus breed on small vertebrate carcasses that range in size from 5-300g, ABBs prefer carrion ranging from 80-100 g (Kozol et al. 1988, Trumbo 1992). This narrow carcass size preference may increase resource scarcity for ABBs since appropriately-sized carcasses may be harder to find than small carcasses and because competition for carrion between ABBs, their congeners and flies increases as carcass size increases (Schnell et al. 2008, Trumbo 1992). Furthermore, larger carcasses are harder and more time consuming to bury. Carcass preference may provide a partial explanation for why ABBs have declined while many of their congeners remain widespread across their ranges (Schnell et al. 2008).

While the ABB has been identified as a habitat generalist, vegetation and soil characteristics may influence food resources and ease of carrion burial (Holloway 1997). The current distribution of ABBs includes populations in Arkansas, Kansas, Massachusetts, Nebraska, Ohio, Rhode Island, South Dakota and Texas. The two largest populations are in

central Nebraska and eastern Oklahoma and western/central Arkansas. In 1991, the USFWS released an ABB recovery plan to reduce the extinction threat. The recovery plan seeks to maintain and protect current populations as well as establish new populations, continue research on the ABB decline and search for new populations (USFWS 1991).

Mesopredator Release

Mesopredators are generally characterized as small to mid-sized species (< 15kg) that fall in the middle of food chains making them both predators and prey. These species can be abundant in the landscape and have a wide range of behaviors, making them an integral part of ecosystems (Roemer 2009). While generally more abundant than apex predators, mesopredators have been considered to have minimal impacts on their surrounding communities in comparison to apex predators (Roemer 2009). Moreover, apex predators have been in decline in many ecosystems worldwide due to habitat loss, hunting, and other factors. The decline in apex predators has also been related to increases in mesopredator abundances; this phenomenon has been described as 'mesopredator release' (Ritchie et al. 2009).

Mesopredator release occurs when mesopredator densities increase as a result of decreased predation pressure from apex predators. Mesopredator release can cause downstream changes in predator-prey relationships leading to changes in ecosystem dynamics (Roemer 2009). For example, Berger and Conner (2008) found in western Wyoming, pronghorn (*Antilocapra americana*) fawn mortality was 34% lower in areas that have an active wolf (*Canis lupus*) population as opposed to those where wolves had been extirpated and coyotes (*Canis latrans*) were the dominant predator. In particular, prey that have low population growth rates or those living in exposed environments where attack by mesopredators is more likely are especially susceptible to mesopredator outbreaks (Ritchie et al. 2009). A consistently negative

relationship between coyote abundance, the apex predator in the studied ecosystem, and mesopredator abundance (Crooks and Soule 1999). In response to a decrease in coyote numbers, the abundance of feral cats, gray foxes (*Urocyon cinereoargenteus*), Virginia opossums, northern raccoons and striped skunks increased (Crooks and Soule 1999). Researchers also found that coyotes in the area had an indirect positive effect on bird diversity due to a reduction in mesopredator predation (Crooks and Soule 1999). Disturbances to ecosystem balance can lead to prey redistributions and scarcity, changes in nutrient abundance and impact lower trophic level communities (Roemer 2009).

Vertebrate Carcass Usage

Mesopredators might impact vertebrate carcass availability in two ways. First, mesopredators may decrease small mammal populations through predation. Also, mesopredators may scavenge carcasses that could be used by ABBs for reproduction. Putnam (1976) found that around 60% of small mammal deaths were caused by direct predation and remaining deaths from other causes were left as carcasses for decomposers and scavengers. Aside from predation, factors such as malnutrition, exposure, disease and other natural causes lead to animal deaths (DeVault et al. 2003). Putnam (1983) suggested that most carcasses were scavenged by vertebrates and causes of animal mortality can be substantially different among different ecosystems (DeVault et al. 2003). For instance, small mammal predation rates might be lower in arctic regions where the harsh environment leads to increased death rates due to exposure or malnutrition (Oksanen et al. 1997). In Colorado, Smith and Merrick (2001) estimated that members of the *Nicrophorus* genus require 1-2% of the average rodent population in carcasses to support the beetle population. As carrion specialists that have a specialized reproductive strategy, ABB populations may be more likely to be influenced by increasing numbers of mesopredators

that scavenge resources. In a study to determine removal rates of carcasses killed by wind turbines in southwestern Germany, Henrich et al. (2017) found that in the summer, 20% of the chick carcasses they placed were buried by beetles in the *Nicrophorus* genus, 40% were taken by vertebrates including both mammals and birds and the other 40% were left unmoved (Henrich et al. 2017). Nearly 67% of the carcasses were taken within 5 days of placement and nearly 40% of those were removed in the first 24 hours (Henrich et al. 2017). Conley (1982) studied how long a species of burying beetle, *Nicrophorus carolinus,* took to locate freshly-placed carcasses and found that it took anywhere from 24 to 100 hours. Rain and strong winds increased location time and habitats that had larger beetle populations decreased location time (Conley 1982). A study in South Carolina examined removal rates of brown rat (*Rattus norvegicus*) and house mouse (*Mus musculus*) carcasses and found that 65% of the carcasses were scavenged within 14 days of placement by northern raccoons, gray foxes and feral pigs (*Sus scrofa*) (DeVault and Rhodes 2002). Furthermore, a later study by DeVault et al. (2004) found northern raccoons and Virginia opossums removed 58% of the placed carcasses, suggesting that these two mesopredator species may be the most likely to compete with ABB for carrion.

Camera Traps

While mark/recapture studies can provide mesopredator density estimates, these techniques are costly and time consuming. Cameras traps have been shown to be a successful tool for detecting mesopredators, as well as other mammal species (Cove et al. 2012). The field of camera trapping has been rapidly growing and this method of detection to be comparable to other methods, if not superior and oftentimes less costly and invasive than other approaches. For example, Nielsen and Cooper (2012) showed that camera traps were more effective than track plates for surveying bobcat (*Lynx rufus*) and coyote populations in Illinois. Another study found

that camera traps were a more efficient method for mesocarnivore detection and occurrence estimates when compared to hair snares (Pedro et al. 2014).

Rowcliffe et al. (2008) developed a technique known as the random encounter model (REM) which allows researchers to estimate densities without identifying individual animals in photographs. The REM uses camera traps to detect animals and takes into account the detection zone of the cameras, animal speed of movement and the number of photographs per unit time to estimate density (Rowcliffe et al. 2008). The model assumes that parts of the landscape which are used preferentially or avoided by animals, for example trails, are sampled in proportion to their coverage on the landscape (Rowcliffe et al. 2014). The REM also assumes that cameras are placed randomly and not baited, both of which can inflate capture rates, or if actively avoided by animals, can decrease capture rates (Rowcliffe et al. 2013). Cameras can operate 24 hours a day and use a passive infrared sensor to detect animals, which allows for large quantities of data collection with minimal effort. Researchers conducted a camera trap study on wallaby (*Macropus rufogriseus*), water deer (*Hydropotes inermis*), muntjac (*Muntiacus reevesi*) and mara (*Dolichotis patagonum*) densities and compared the REM densities to census data. They found that when compared to raw trapping rate densities, the camera trapping rates were more strongly correlated with census data densities ($R^2 = 0.76$) (Rowcliffe et al. 2008). Estimates for density from camera trap pictures showed that no strong bias was evident and supported the effectiveness and accuracy of the random encounter model (Rowcliffe et al. 2008).

After Rowcliffe's 2008 random encounter model was released, other researchers conducted further research on the model. Estimates of lion (*Panthera leo*) density in the Serengeti National Park compared the REM density estimate to estimates from census data. They found that when the assumptions were met the REM provided an unbiased density estimate and

was more precise and/or less time consuming than other methods such as distance sampling and sight-resight methods (Cusack et al. 2015). In addition, a study on pine marten (*Martes martes*) density in Italy compared three density estimation methods including: camera trapping, hair tubes and scat surveys. They found that camera trapping incorporating the REM to estimate densities was the only method that both assessed presence and provided an accurate population density estimate (Bartolommei et al. 2012). A 2017 study by Chauvenet et al. looked at the bias associated with camera trapping with REM methods to study wild boar. They found that the REM both over and under-estimated density estimates based on group size so the method may be better suited for non-social animals. Researchers determined that bias can be reduced by improving survey design by gathering more data over a larger monitoring area, ensuring random camera placement, and sampling different habitat types to account for heterogeneity (Chauvenet et al. 2017).

Habitat Fragmentation

Land use changes due to human practices can significantly alter community composition (Eagan et al. 2011). A major consequence of habitat fragmentation is a decrease in specialist predator populations and an increase in generalist mesopredators, which can negatively impact small mammal populations due to predation. Specialist predator populations often cannot survive or experience significant population reductions in altered or fragmented landscapes (Eagan et al. 2011). Crooks (2002) showed that predators such as mountain lions (*Puma concolor*), bobcats and coyotes were more sensitive to fragmentation and their populations decreased as fragment size decreased. However, smaller species such as feral cats, gray foxes and Virginia opossums increased in distribution and abundance as fragment size decreased (Crooks 2002). The Midwestern United States has seen a major decrease in forested land (up to an 88% decrease

since European settlement), which has been cleared and repurposed to grow crops (Eagan et al. 2011). Eagan et al. (2011) found that white-footed mice (*Peromyscus leucopus*) numbers were higher in fragmented areas where northern raccoons had been removed suggesting that irregular mesopredator abundance due to landscape changes can limit prey species and alter trophic dynamics. Furthermore, DeVault's (2004) study found that vertebrates removed a much higher percentage of the rodent carcasses in the winter (49%) as opposed to the summer (17%). Therefore, interactions between mesopredators and ABBs may be particularly important during the active season of ABBs and the impact of seasonal or even daily temperature variations can affect decomposer activity.

Habitat fragmentation has been referred to as the ultimate factor causing an increase in vertebrate competition for carrion and a reduction in optimally sized carrion throughout the historical range of the ABB (USFWS 2015). Creighton et al. (2009) found ABBs declined in areas of forest removal in Oklahoma and proposed that the decline may have been a result of a change in the mammal community composition. Trumbo and Bloch (2000) investigated forest fragments and concluded that various burying beetles (*Nicrophorus* spp.) had higher success rates in large woodland plots, potentially due to a reduction in the success of vertebrate scavengers.

Study Site

Fort Chaffee Joint Maneuver Training Center (FCJMTC) is a 64,247 acre military base located in western Arkansas and has the largest known population of ABBs in the state. FCJMTC is located mainly in the Arkansas River Valley and the southeastern tip of the base extends into the Ouachita Mountains. The base has active military training and there are three basic land use categories including: improved, semi-improved and unimproved. Improved areas

include structures, buildings and cemeteries, while semi-improved areas are predominantly landing strips and storage areas, and unimproved areas are agricultural leases and range training areas (ARARNG 2001). A network of paved, gravel and dirt roads runs across FCJMTC to provide access and there are many lakes, ponds and streams on the base. While the western side of the base houses military and administration buildings as well as many training areas, the eastern side of the base is a wildlife management area and is open to the public for recreation at certain times of year. FCJMTC is an ideal place to study wildlife because much of the terrain has been left undisturbed or is actively managed for game species and controlled burns are conducted to reduce fuel buildup or restore unique habitats such as prairies.

FCJMTC has many unique habitats including cedar, pine, oak, shrub land, developed, deciduous, grassland/ prairie, lespedeza and bottomland hardwood. In addition to the ABB, FCJMTC and the surrounding region is home to numerous species of mesopredators including: bobcats, northern raccoons, Virginia opossums, coyotes, eastern spotted skunks (*Spilogale putorius*), striped skunks, mink (*Neovison vison*), gray foxes and red foxes (Sealander and Heidt 1990). The military base also falls into the known range of apex predators including: black bears (*Ursus americanus*), red wolves (*Canis rufus*) and mountain lions (Sealander and Heidt 1990). However, red wolves and mountain lions are currently not present. A 1991 survey at FCJMTC identified black bears alongside numerous mesopredators (Sturdy et al. 1991). FCJMTC is an ideal research site that has diverse habitats and provides the opportunity to compare ABB and mesopredator abundances in order to explore trends and/or relationships between the two groups and assess their distributions across the landscape.

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CHAPTER 1: MESOPREDATOR ABUNDANCE AND DISTRIBUTION AT FORT CHAFFEE JOINT MANEUVER TRAINING CENTER ESTIMATED FROM CAMERA TRAP DATA

Mesopredators are small to mid-sized species (< 15kg) that fall in the middle of food webs making them both predators and prey for larger species. Mesopredators can be abundant in the landscape and have a wide range of behaviors, making them an integral part of ecosystems. Although often more abundant than apex predators, mesopredators have usually been considered to have minimal impacts on their surrounding communities in comparison to apex predators (Roemer 2009). Moreover, apex predators have been found to be in decline in many ecosystems worldwide due to habitat loss, hunting, and other factors. The decline in apex predators has also been related to increases in mesopredator abundances; this phenomenon has been described as 'mesopredator release' (Ritchie et al. 2009).

Mesopredator release occurs when mesopredator densities increase as a result of decreased predation pressure from apex predators. Mesopredator release can cause downstream changes in predator-prey relationships leading to changes in ecosystem dynamics (Roemer 2009). For example, Berger and Conner (2008) found that in western Wyoming pronghorn fawn (*Antilocapra americana*) mortality was 34% lower in areas that have a prevalent wolf (*Canis lupus*) population as opposed to those where wolves had been extirpated and coyotes (*Canis latrans*) were the dominant predator. In particular, prey that have low population growth rates or those living in exposed environments where attack by mesopredators is more likely are especially susceptible to mesopredator outbreaks (Ritchie et al. 2009). A consistently negative relationship between coyote abundance, the apex predator in the ecosystem, and mesopredator abundance has also been documented (Crooks and Soule 1999). Reduced coyote numbers led to

an increased abundance of feral cats (*Felis catus*), gray foxes (*Urocyon cinereoargenteus*), Virginia opossums (*Didelphis virginiana*), northern raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) (Crooks and Soule 1999). Researchers also found that coyotes in the area had an indirect positive effect on bird diversity due to a reduction in mesopredator predation (Crooks and Soule 1999). Disturbances to ecosystem balance can lead to prey redistributions and scarcity, changes in nutrient abundance and impact lower trophic level communities (Roemer 2009).

Furthermore, mesopredator release and subsequent increased predation on small vertebrates and/or increased scavenging pressure has been hypothesized as a cause of decline of the American burying beetle (*Nicrophorus americanus,* hereafter ABB*)* decline. Listed as an endangered species in 1989, ABBs are carrion specialists and require small animal carcasses for successful reproduction (Walker 2007). Sikes and Raithel (2002) proposed an increase in mesopredator numbers could negatively impact ABB populations due to increased competition between vertebrate scavengers and ABBs for carcasses. Mesopredators such as the northern raccoon, Virginia opossum, coyote, bobcat (*Lynx rufus*), common gray fox and red fox (*Vulpes vulpes*) would be likely competitors for carrion (Sikes and Raithel 2002). A study in South Carolina examined removal rates of brown rat (*Rattus norvegicus*) and house mouse (*Mus musculus*) carcasses and found that 65% of the carcasses were scavenged within 14 days of placement by northern raccoons, gray foxes and feral pigs (*Sus scrofa*) (DeVault and Rhodes 2002). Furthermore, a later study by DeVault et al. (2004) found that northern raccoons and Virginia opossums removed 58% of the placed carcasses, suggesting that these two mesopredator species may be the most likely to compete with ABB for carrion.

In Arkansas, coyotes, bobcats, Virginia opossums, common gray foxes, red foxes and northern raccoons are commonly encountered mesopredators (Sealander and Heidt 1990). Coyotes are found in all of Arkansas but they may be especially common in western Arkansas (Sealander and Heidt 1990). They typically inhabit open habitats such as fields, shrublands and forest edges (Sealander and Heidt 1990). Coyote diets are diverse, ranging from berries to deer carrion, and small mammals (Sealander and Heidt 1990, Swingen et al. 2015). Bobcats are found statewide in Arkansas and inhabit a variety of habitats from bottomland forests to grasslands but they show a preference for rocky outcrops (Sealander and Heidt 1990, Rucker et al. 1989). They feed predominantly on rabbits and small rodents but they will scavenge on carcasses of deer when able (Sealander and Heidt 1990). Virginia opossums are abundant everywhere in Arkansas and inhabit woodland areas with a preference for bottomland forests (Sealander and Heidt 1990). They are omnivorous, opportunistic foragers (Sealander and Heidt 1990). Northern raccoons are common across Arkansas and while they prefer bottomland hardwood habitats, they are found in a variety of woodland and farmland habitats (Sealander and Heidt 1990). They are omnivorous, opportunistic foragers with diets ranging from acorns to insects and small mammals and they have adapted well to living in urban areas (Sealander and Heidt 1990). Apex predators including mountain lions (*Puma concolor*) and black bears (*Ursus americanus*) were once found statewide in Arkansas but mountain lions have been extirpated from the state and although black bears were extirpated they were reintroduced to the Ouachita and Ozark Mountains (AGFC 1998).

Land use changes driven by human practices have greatly altered community composition across a vast portion of the United States (Eagan et al. 2011). The Midwestern United States has seen a major decrease in forested land (up to an 88% decrease since European settlement), which has been cleared and repurposed to grow crops (Eagan et al. 2011). One

consequence of habitat fragmentation has been a decrease in specialist predator populations and an increase in generalist mesopredators, which has been linked to declines in small mammal populations due to predation (Eagan et al. 2011). Multiple mechanisms have been proposed to explain changes in predator distribution and inflated abundance of some species in fragmented and edge habitats including: increased prey availability or diversity, ease of travel, increased foraging efficiency, and edge habitat specialization (Lidicker 1999, Lariviere 2003, Lariviere and Messier 2000, Svobodova et. al 2010). While generalist mesopredators often thrive, specialist apex predators often cannot survive or exist at significantly reduced population levels in altered or fragmented landscapes (Eagan et al. 2011). Cervinka et al. (2011) found that domestic cats, red foxes, martens, least weasels and Eurasian badgers preferred edge habitat and their occurrence was negatively correlated with fragment size. Crooks (2002) showed that relative abundances of Virginia opossums and northern raccoons was either unaltered or enhanced by fragmentation while coyotes and bobcats were sensitive to fragmentation and relative abundances decreased. Crooks (2002) found that apex predators such as mountain lions (*Puma concolor*) were more sensitive to fragmentation and their populations decreased as fragment size decreased. On the other hand, species such as feral cats, common gray foxes and Virginia opossums increased their distribution and abundance as fragment size decreased (Crooks 2002).

Use of camera traps in wildlife studies has become more popular because it is often less costly and time consuming than traditional trapping/ tracking methods and equally or more effective (Nielsen and Cooper 2012). Rowcliffe et al. (2008) developed a technique known as the random encounter model (REM), which allows researchers to estimate densities without identifying individual animals in photographs. The REM uses camera traps to detect animals and takes into account the detection zone of the cameras, animal speed of movement and the number

of photographs per unit time to estimate density (Rowcliffe et al. 2008). This methodology has been shown to be effective and accurate in multiple studies that compared known population sizes from censuses to REM estimates (Cusak et al. 2015, Rowcliffe et al. 2008). The REM model has been criticized for potentially generating biased density estimates because the assumption of random and independent animal movements may not be realistic and because determination of specific input parameters for the model, including speed of movement can be difficult to estimate (Rovero and Marshall 2009, Foster and Harmsen 2012). Foster and Harmsen (2012) also argue that the model can be restrictive by requiring random placement of cameras. While Rovero and Marshall (2009) acknowledge the difficulty in determining REM parameters they conclude that estimates from transect counts and other methods can also be inaccurate due to poor detectability and factors such as nocturnal activity reducing sightings that trail cameras are able to capture. Rowcliffe et al. (2013) clarified that although random movement is an assumption of the model, violations will not bias density estimates. Furthermore, they explain that for the REM method to be effective the cameras need not necessarily be entirely random but rather sample features in the area in proportion to their coverage on the landscape and not inflate estimates by placing all cameras on trails or known feeding areas (Rowcliffe et al. 2013).

Fort Chaffee Joint Maneuver Training Center (FCJMTC) is a military base located in western Arkansas. The base and surrounding land is home to numerous species of mesopredators including: bobcats, northern raccoons, Virginia opossums, coyotes, striped skunks, mink (*Neovison vison*), common gray foxes and red foxes (Sealander and Heidt 1990). A population of ABBs is also present on the base and yearly censuses have been conducted since 1992 (FTN 2017). FCJMTC contains a variety of habitat types including: cedar, pine, oak, shrubland, developed, deciduous, grassland/ prairie, lespedeza and bottomland hardwood. Farmland, roads

and urban sprawl surround the border of the military base. A predator study conducted at FCJMTC from 2003 to 2005 used camera traps and hair snares to study mammalian predators. Camera effort totaled 1,069 functional nights but the only predators detected were two northern raccoons and two coyotes. The researchers recommended continued research and greater camera trap effort (ARARNG 2005). FCJMTC provides a unique opportunity to study mesopredators and ABBs in area where both co-occur.

Objectives:

1. Assess the relative abundances of mesopredators (Virginia opossums, northern raccoons, coyotes and bobcats) at FCJMTC.
2. Assess the relative abundance of mesopredators in different habitats present at FCJMTC.
3. Determine density estimates across different habitat types for mesopredators at FCJMTC from the REM.
4. Determine whether mesopredator relative abundances at FCJMTC change in relation to distance from the base edge.
5. Determine if relationships exist between mesopredator abundance and ABB abundance at FCJMTC.

I hypothesize that there will be associations between specific habitat types and mesopredator species at FCJMTC based on previously cited habitat preferences in Arkansas (Sealander and Heidt 1990). In addition, I hypothesize that REM will provide density estimates that are reasonable and consistent with other abundance estimates determined in the region. Furthermore, I hypothesize that there will be an increased number of mesopredators, especially northern raccoons and Virginia opossums, near the edges of the FCJMTC because their numbers

can increase in fragmented landscapes and the land surrounding the base is fairly developed (Crooks 2002). Based on the carrion competition hypothesis, I predict that there will be fewer mesopredator captures in the area of greatest ABB abundance.

METHODS

Study Site

I conducted this study at FCJMTC in central-western Arkansas (Figure 1.1). FCJMTC consists of approximately 25,090 hectares (261 km^2) located primarily within the Arkansas River Valley ecoregion just east of Fort Smith in Sebastian, Crawford, and Franklin Counties. Extreme southern portions of the FCJMTC base are located within the Ouachita Mountain ecoregion. I sampled nine different habitat types at FCJMTC including: cedar, pine, oak, shrub land, developed, deciduous, grassland/ prairie, lespedeza and bottomland hardwood. The largest portion of FCJMTC is comprised by oak habitat at 29%, followed by 19.5% bottomland hardwood, 13% deciduous, 9% cedar, 8% lespedeza, 7.5% grassland/ prairie, 5.5% shrubland, 5% developed/ water features and 3.5% pine (Figure 1.2). The habitats, which are of varying patch sizes, are distributed across FCJMTC. Average rainfall at FCJMTC is 107 cm and May and June generally see the most rainfall (Cox et al. 1975). In 2017, the highest temperature in the area was 37 °C in July and the highest mean monthly temperature was 34.1 °C in July. The lowest temperature was -14.4 °C in January and the lowest mean monthly temperature was 0.94 °C (SERCC 2017). A variety of soil types exist which exhibit a varied distribution at FCJMTC from 3 to 35% clay to 15 to 75% sand and 20 to 65% silt (Lomolino et al.1995).

Study Species

In Arkansas, common mesopredators include striped skunks, coyotes, Virginia opossums, red foxes, common gray foxes and northern raccoons. Nupp (2007) recorded trapping or

observing northern raccoons, Virginia opossums, coyotes, striped skunks and bobcats among other species at FCJMTC.

Camera Traps

I collected data during two field seasons: summer 2017 (June to August) and summer 2018 (June to August). I used the random point generator tool in ArcMap Version 10.3.1 to choose camera trap locations in each of the nine different habitat types. I placed 81 camera traps, distributed among habitat types in proportion to the area of each habitat type. The number of cameras in a habitat varied from 3 traps in pine habitat to 20 in oak habitat. Traps were set to take photos at each site for two to four weeks and then moved to another site. I was restricted in moving camera traps due to coordination with ongoing military maneuvers. Cameras were placed 50 m to 100 m from roads so they were easily accessible but not directly on roads and they were placed 0.5 m to 1 m off the ground on trees or posts. Mesopredators and their carcasses are commonly observed along roadways (Nielsen et al. 2012) so a 50 m buffer was placed around roads in ArcGIS to ensure cameras were not placed directly on roads to avoid artificially inflating captures. Camera trap coordinates were transferred from ArcMap to a GPS (Trimble™ Geo7X) to ensure cameras could be placed accurately at randomly-selected site locations. I did not bait camera traps to avoid interference with ABB breeding and activity as well as to ensure trapping rates were not artificially inflated.

Camera traps have been found to be a successful tool for detecting mesopredators, as well as other mammal species (Cove et al. 2012). The Spypoint Force® 10 cameras I used operate 24 hours a day and use a passive infrared sensor (PIR) to trigger the camera to take photos. The PIR sensor was able to detect IR radiation that was emitted from objects passing through the camera's detection zone. The sensor can detect an object's surface temperature and rapid

temperature changes cause the pyroelectric elements in the sensor to produce a current that triggers the camera (Welbourne et al. 2016). In a thermally heterogeneous environment, objects moving in the background, such as branches swaying in the wind, can cause false-triggers. The air temperature has no effect on the passive infrared sensors and the sensors can detect both increases and decreases in temperature (Welbourne et al. 2016). The cameras had a 0.32 second trigger speed with a 0.52 s recovery time between pictures, and up to 24 m detection range and 42 LEDs for nighttime illumination.

To determine mesopredator relative abundance across different habitat types at FCJMTC, I counted the number of animals photographed by the camera traps and recorded species, time and location to the best of my ability. Individuals that I was unable to identify to species were recorded as 'other'. In order to avoid double counting of individual animals, if it was clear the animal was present in subsequent frames it was only recorded once and if the same species was seen at one location within a period of 30 minutes it was excluded to ensure events were independent (Tobler et al. 2008, Kelly and Holub 2008).

I examined the potential impact of edge effects on mesopredator abundances by examining the distance from trap sites to the edges of FCJMTC because farmland and houses were past the border of the base. I used the near tool in ArcGIS version 10.3.1 to measure distance of each camera trap location to the nearest edge of FCJMTC and then determined whether there was a relationship between mesopredator abundances and distance. In order to assess if there was overlap between ABB and mesopredator ranges on FCJMTC a high ABB zone convex polygon that connected ABB sites that had ABB captures higher than the mean was generated in ArcGIS by using the minimum bounding geometry data management tool. ABB

data was taken from FTN Associates Ltd. yearly ABB census reports (FTN 2017, FTN 2018). A polygon was created for both 2017 and 2018 seasons.

To determine mesopredator abundance across different habitat types at FCJMTC, I used the random encounter model (REM) to estimate density from camera trapping rates (Rowcliffe et al. 2008). This method requires knowing the detection zone of the cameras, animal speed of movement and the number of photographs per unit time (Rowcliffe et al. 2008). The detection zone of the cameras was determined by drawing an enlarged protractor in an open area and marking varying distances (1m, 3m, 5m 10m, 15m) that were visible on the pictures. The farthest angle visible in the photos was used for the detection angle, as many animals were visible at the edges of the photo. Then, the distance from the bottom of the photo to the measurement marking was calculated for 90 degrees and 75 degrees. Measurements were taken of the mesopredators in each photo from the bottom of the photo to the foot of the mesopredator and angles were estimated based on placement in the photo. Mesopredator measurements and angle estimates were compiled and z-scores were calculated to determine the maximum detection distance at the 95% confidence level. Animal speed of movement was determined from consulting gps and telemetry studies in the literature for each species (Table 1.9). The REM equation that was used to obtain density estimates is as follows:

$$D = \frac{\gamma}{t} * \frac{\pi}{Vr(2 + \theta)}$$

Where y is the number of independent photographic events, t is the total camera survey effort, V is average speed of animal movement, r and θ are the radius and angle of the camera trap detection zone (Cusack et al. 2015). The model assumes that parts of the landscape which are used preferentially or avoided by animals, for example trails, are sampled in proportion to their coverage on the landscape (Rowcliffe et al. 2014). The REM also assumes that cameras are

placed randomly and are not baited or avoided by animals (Rowcliffe et al. 2013). These assumptions were met by randomly placing the cameras in different habitat types and ArcGIS version 10.3 was used to randomly generate points. If a trail was present in the location of the random point then the camera was pointed toward the trail or opening but if no trail was present I did not actively seek out a trail to place the camera on as this may have inflated capture numbers and interfered with an REM assumption.

Data Analysis

From the camera data and the REM procedure I determined estimates of mesopredator abundance within each habitat type on FCJMTC. The Shapiro-Wilks test was run in addition to visually assessing distribution data to evaluate for normality. I attempted Box-Cox transformations in order to make the data fit a normal distribution, but the transformed data did not conform to normality for either year based upon the ANOVA output plots. Therefore, I checked for equal variance and then ran a Kruskal-Wallis test to compare mesopredator abundances among the different habitats. Alpha was set to 0.05 for all tests.

I also grouped the habitats into open (composed of lespedeza, shrubland, grassland/ prairie and developed) and woodland (composed of oak, cedar, pine, bottomland hardwood and deciduous) groups and ran a Kruskal-Wallis test to determine if mesopredator species were found more often in either open or woodland habitats to determine if this corresponds to the literature on habitat use. To determine if Virginia opossum, northern raccoon and bobcat abundances varied among the habitats, I removed coyote captures and repeated a Kruskal-Wallis test.

Program Presence Version 12.7 was used to estimate the portion of the area occupied by mesopredator species. This program accounts for the fact that while species may be present, they

may not be detected by the camera traps. A high ABB polygon was generated from ABB census data and a Wilcoxon Rank Sum test was conducted on mesopredator captures between sites inside and outside the high ABB zone. A zero-inflated negative binomial regression (ZINB) was conducted to evaluate whether a relationship existed between mesopredator abundances and distance to the edge of FCJMTC. The ZINB was run due to lack of normality, overdispersion and an abundance of sites in which no mesopredators were photographed. Mesopredator counts per trap night were converted to integers for the ZINB by multiplying by 100 and rounding to the nearest whole number, which resulted in values showing mesopredator counts per 100 trap nights.

RESULTS

Mesopredator Abundances

I photographed 667 independent animal sightings in 2017 during 1,135 trap nights and 661 independent animal sightings in 2018 during 941 trap nights. Over the two seasons, 160,042 photos were collected at 81 camera sites (Figure 1.5, 1.8) in nine habitat types and 147,357 of those were false-triggers, meaning something other than an animal, such as leaves moving in the wind, triggered the camera (Table 1.1). Photos from three camera sites were deemed unusable leaving 78 usable sites. Pictures of over 15 different species were collected; white-tailed deer were the most commonly observed species (Table 1.2). Commonly captured mesopredators included Virginia opossums, northern raccoons, coyotes and bobcats (Figure 1.6 and 1.9). Overall, these mesopredators made up 9% of the 1,328 independent animal sightings. Coyotes were the most captured mesopredator at 60 (50%) independent sightings followed by northern raccoons, bobcats and Virginia opossums at 37 (31%), 12 (10%) and 11 (9%) independent sightings respectively (Figure 1.11 and Table 1.2).

Oak habitat was the dominant habitat type at FCJMTC and therefore received the most camera traps (20), while pine habitat was the least common and received 3 camera traps (Figure 1.3). Oak habitat had the most usable trap nights collected and lespedeza habitat had the least number of usable trap nights collected (Figure 1.4). Cameras where the photos went black or the camera fell over or off the tree were not used. Most mesopredator sightings were in the bottomland hardwood, oak and deciduous habitats. There were fluctuations in mesopredator sightings between the two years for all four mesopredator species (Figures 1.12 to 1.15).

Differences in mesopredator abundance among the nine habitat types did not meet the assumption of normality ($W=0.274$, $p<0.001$). A Kruskal-Wallis test did not show significant differences in mesopredator captures per trap night in the nine habitat types (oak, bottomland hardwood, deciduous, lespedeza, shrubland, grassland/ prairie, cedar, developed and pine) in 2017 ($\chi^2 = 5.49$, $p = 0.704$, $df = 8$) or in 2018 ($\chi^2 = 11.076$, $p = 0.197$, $df = 8$). In 2017 no differences were detected between captures in the woodland and open habitat groups for Virginia opossums ($\chi^2 = 0.37$, $p = 0.54$, $df = 1$), northern raccoons ($\chi^2 = 0.01$, $p = 0.899$, $df = 1$), coyotes ($\chi^2 = 0.81$, $p = 0.37$, $df = 1$), or bobcats ($\chi^2 = 2.07$, $p = 0.15$, $df = 1$). In 2018 no differences were detected between captures in the woodland and open habitat groups for Virginia opossums ($\chi^2 = 2.29$, $p = 0.13$, $df = 1$), northern raccoons ($\chi^2 = 2.81$, $p = .09$, $df = 1$), coyotes ($\chi^2 = 0.81$, $p = 0.37$, $df = 1$), or bobcats ($\chi^2 = 1.30$, $p = .25$, $df = 1$). No differences were detected between captures in the woodland and open habitat groups when seasons were combined for Virginia opossums ($\chi^2 = 2.52$, $p = 0.11$, $df = 1$), northern raccoons ($\chi^2 = 2.03$, $p = 0.15$, $df = 1$), coyotes ($\chi^2 = 1.66$, $p = 0.20$, $df = 1$), or bobcats ($\chi^2 = 3.44$, $p = 0.06$, $df = 1$). When the four species and seasons were combined, more mesopredators were captured per trap night in the wooded habitat group ($\chi^2 = 6.11$, $p = 0.01$, $df = 1$, $\bar{x} = 0.07$, $SE = 0.03$).

I made similar comparisons among habitats while excluding coyotes because 50% of the independent sightings were coyotes but the literature indicates raccoons and opossums may be the most likely to compete for carrion resources (DeVault et al. 2004) and I was concerned that multiple coyote sightings at a single camera site inflated the values. A Kruskal-Wallis Test that examined the difference in mesopredator abundance among the nine habitat types excluding coyotes showed no significant differences in mesopredator captures per trap night among the habitat types in 2017 ($\chi^2 = 5.22$, $p = 0.734$, $df = 8$), 2018 ($\chi^2 = 11.0$, $p = 0.201$, $df = 8$) or when combined ($\chi^2 = 10.83$, $p = 0.21$, $df = 8$). When the habitat types were grouped and seasons were combined, more mesopredators were captured per trap night in the wooded habitat group ($\chi^2 = 5.68$, $p = 0.02$, $df = 1$, $\bar{x} = 0.03$, $SE = 0.01$).

REM Density Estimates

I was able to calculate REM density estimates for coyotes, northern raccoons, bobcats and Virginia opossums for both 2017 and 2018. Gray foxes were not seen often enough to calculate density estimates because only two independent captures were recorded. In each year zero mesopredators were captured in the lespedeza habitat so density estimates were 0 animals/km for all mesopredators both seasons in this habitat.

Coyote density estimates in 2017 were highest in the bottomland hardwood, developed and oak habitats (2.31 coyotes/km^2, 0.57 coyotes/km^2 and 0.44 coyotes/km^2 respectively) (Table 1.3). In 2018, coyote density estimates were highest in the grassland/ prairie, oak and bottomland hardwood habitats (1.08 coyotes/km^2, 1.06 coyotes/km^2, and 0.47 coyotes/km^2, respectively) (Table 1.4). Over the two seasons, coyote densities were highest in the bottomland hardwood, oak and grassland/ prairie habitats (1.53 coyotes/km^2, 0.73 coyotes/km^2 and 0.45 coyotes/km^2 respectively) and no coyotes were captured in the lespedeza and pine habitats (Table 1.5). Bobcat

density estimates in 2017 were highest in the oak, bottomland hardwood and deciduous habitats (0.28 bobcats/km^2, 0.19 bobcats/km^2 and 0.17 bobcats/km^2 respectively) (Table 1.3). In 2018, bobcat density estimates were highest in the bottomland hardwood and oak habitats (0.51 bobcats/km^2, 0.08 bobcats/km^2) and no bobcats were seen in any of the other habitat types (Table 1.4). Over the two seasons, bobcat densities were highest in the bottomland hardwood, oak and deciduous habitats (0.32 bobcats/km^2, 0.19 bobcats/km and 0.17 bobcats/km^2 respectively) and no bobcats were captured in the lespedeza, shrubland, grassland/ prairie, cedar, developed or pine habitats (Table 1.5).

In 2017, northern raccoon density estimates were highest in the developed, oak and cedar habitats (2.10 raccoons/km^2, 1.08 raccoons/km and 0.67 raccoons/km^2 respectively) (Table 1.3). In 2018, northern raccoon density estimates were highest in the bottomland hardwood, oak and deciduous habitats (7.53 raccoons/km^2, 2.32 raccoons/km^2 and 1.19 raccoons/km) (Table 1.4). Over the two seasons, northern raccoon densities were highest in the bottomland hardwood, oak and developed habitats (3.19 raccoons/km^2, 1.65 raccoons/km and 1.25 raccoons/km^2 respectively) and no raccoons were captured in the lespedeza, shrubland, grassland/ prairie, or pine habitats (Table 1.5). In 2017, Virginia opossum density estimates were only calculated in the oak habitat (2.05 opossums/km^2) because there were no captures in any of the other habitat types (Table 1.3). In 2018, Virginia opossum density estimates were highest in the deciduous, bottomland hardwood and oak habitats (11.33 opossums/km^2, 1.88 opossums/km^2, 0.61 opossums/km^2) and no Virginia opossums were seen in any of the other habitat types (Table 1.4). Over the two seasons, Virginia opossum densities were highest in the deciduous, oak and bottomland hardwood habitats (3.79 opossums/km^2, 1.40 opossums/km^2 and 0.80 opossums/km^2

respectively) and no Virginia opossums were captured in the lespedeza, shrubland, grassland/ prairie, cedar, developed or pine habitats (Table 1.5).

Program Presence Psi Estimates

Program presence generated psi estimates that were highest for Virginia opossums in 2018 (ψ=0.208), northern raccoons in 2017 (ψ=0.158), coyotes in 2018 (ψ=0.462) and bobcats in 2017 (ψ=0.276) (Tables 1.6 and 1.7). Overall, the psi value was the highest for coyotes in 2018 (ψ=0.462) and the lowest for Virginia opossums in 2017 (ψ=0.028). Habitat types with the highest psi estimates for Virginia opossums, coyotes and bobcats included bottomland hardwood and oak while deciduous and bottomland hardwood had the highest psi estimates for northern raccoons.

High Density ABB Area

The mean number of ABB captures per bucket trap site from the yearly ABB census was 5.7 ABBs in 2017 and 4.4 ABBs in 2018 (FTN 2017, FTN 2018). A Wilcoxon Rank Sum test was conducted between sites inside and outside the high ABB zone and mesopredator per trap day counts because the data were not normally distributed (Shapiro-Wilk Test in 2017 ($W=0.274$, $p<0.001$) and 2018 ($W=0.466$, $p<0.001$)). No significant differences were found between mesopredator captures per trap night inside and outside the high ABB zone in 2017 ($W=116$, $p=1$) or 2018 ($W=105.5$, $p=0.503$) (Figures 1.7 and 1.10).

Edge Effects

In 2017, the ZINB regression count model showed there was a negative relationship between mesopredator counts per 100 trap nights and distance to the edge of the base (estimate = -0.0007, SE = 0.0003, p= 0.07) but the zero-inflation model showed no relationship (estimate = -0.0001, SE = 0.001, p= 0.93). In 2018, the ZINB regression count model showed there was a

negative relationship between mesopredator counts per 100 trap nights and distance to the edge of the base (estimate = -0.0005, SE = 0.0002, p= 0.02) but the zero-inflation model showed no relationship (estimate = -0.0001, SE = 0.0006, p= 0.79). When the seasons were combined, the ZINB regression count model showed there was a negative relationship between mesopredator counts per 100 trap nights and distance to the edge of the base (estimate = -0.0006, SE = 0.0002, p= 0.003) but the zero-inflation model showed no relationship (estimate = -0.0001, SE = 0.0006, p= 0.841).

DISCUSSION

Mesopredator Density Estimates

In general, density estimates calculated from the REM fell within density ranges found from previous studies but I was unable to produce density estimates for some species in several habitat types because of low capture rates (Tables 1.3, 1.4). No mesopredator photos were captured in the lespedeza habitat type in either study season. This lack of sighting may be attributed to the structure of the habitat vegetation. The tall, dense vegetation decreases the camera detection range and moving vegetation leads to false-triggers. Numerous deer were captured in the lespedeza habitat but mesopredators, especially Virginia opossums and northern raccoons are much smaller and can be easily undetectable behind dense vegetation. As species size decreases, the probability of capture by the camera trap decreases (Tobler et al. 2008).

The zone of camera detection area was not equal across all of the habitat types so camera survey effort varied across habitat types as well as the number of cameras that were placed in each habitat type. If this study were replicated, the area of the zone of detection should be taken into account when determining how many cameras to place in each habitat type rather than just placing cameras in proportion to habitat coverage across the base. This would account for the

fact that the area surveyed by each camera in a densely vegetated habitat such as the lespedeza habitat is smaller than the area surveyed in an open habitat such as the bottomland hardwood habitat. In addition, larger animals triggered the camera traps over a larger detection range in comparison to smaller animals. A pilot study could be conducted to assess the size of the camera detection zone in each habitat for different species through on the ground experimentation and evaluation of camera trap photos. Home ranges and habitat coverage on the study site could also be evaluated to determine necessary camera effort. For example, bobcat home range in western Arkansas was estimated to be 24.5 km^2 for female bobcats (Rucker et al. 1989) and the bottomland hardwood habitat covers 40 km^2 of FCJMTC so 2 camera traps in the habitat may effectively capture bobcat presence.

Virginia opossum densities calculated from the REM ranged from 0.8 to 3.79 animals/km^2, which fall within the range reported by other Virginia opossum studies (1.1-12.3/km^2; Fitch and Sandidge 1953, Seidensticker et al. 1987, Kissell and Kennedy 1992, Gehrt et al. 1997, Kasparian et al. 2004, Beatty et al. 2016) for the oak and deciduous habitats (Table 1.5). The Kasparian et al. (2004) study was probably most comparable to my western Arkansas location. Their study site was in central Oklahoma in a region similar to that of FCJMTC and they estimated Virginia opossum density at 2/km^2, which is near my FCJMTC estimates. My density estimate for the bottomland hardwood habitat density estimate (0.80 animals/km^2) was lower than expected and the other habitat types not stated previously (0 animals/km^2) fall below the density estimates cited in the literature and this may be attributed to low capture rates of Virginia opossums at sites because the sites were not baited. Allen et al. (1985) found Virginia opossums tended to forage near streams and travel among foraging patches in areas with high cover rather than take shorter routes through open fields. Gipson and Kamler (2001) found

coyotes were responsible for 65% of the Virginia opossum deaths in their study in a tall grass prairie ecosystem. Coyotes accounted for 50% of the total mesopredator independent captures at FCJMTC, which suggests Virginia opossums may be vulnerable to these predators. Findings suggest Virginia opossum captures could be low due to foraging habits and movements in heavy cover to avoid easy detection by predators.

Northern raccoon REM density estimates ranged from 0.31 to 3.19 animals/km^2 depending on the habitat type, which falls within the density estimates from 2.2-15.3 animals/km^2 reported by other studies (Nottingham et al. 1989, Rosatte et al 2010, Johnson 1970, Woods 1978, Keeler 1978, Kissell and Kennedy 1992) for the bottomland hardwood habitat and below reported estimates for all other habitat types (Table 1.5). The 1992 study by Kissell and Kennedy was conducted in western Tennessee and they found 1.42-2.9 raccoons/km^2 depending on the study site. The Kissell and Kennedy (1992) study falls in a similar region as FCJMTC and density estimates are similar.

Coyote REM density estimates ranged from 0.11 to 1.53 animals/km^2 depending on the habitat type, which falls within density estimates from 0.1 to 1.37 found in the literature (Hein and Andelt 1995, Babb and Kennedy 1989, Pyrah 1984, Andelt 1985, Camenzind 1978) for all habitats except the bottomland hardwood, lespedeza and pine (Table 1.5). The bottomland hardwood habitats had a high density estimate (1.53 animals/km^2) that can be attributed to one camera site that had 27 independent sightings but these were likely repeated sightings of the same coyotes and this artificially inflated the density estimate.

Bobcat density estimates ranged from 0.12 to 0.32 animals/km^2 depending on the habitat type, which falls within density estimates from 0.06-1.25 animals/km^2 for the bottomland hardwood, oak and deciduous habitats (Table 1.5). Higher bobcat densities have been observed

in the southeastern part of the US (0.61-2 animals/km^2; Provost et al. 1973, Conner 1982) while estimates are lower for Arkansas (0.06-.11; Hamilton 1982, Rolley 1985, Rucker et al. 1989, Kitchings and Story 1984).

Difficulties encountered in estimating densities from the REM across habitats included low detectability, false-triggers and velocity estimates. The low detection rates at non-baited camera trap sites made calculating density estimates for certain habitats impossible and led to questions on whether species, such as Virginia opossums, were present but not frequently detected by cameras. Virginia opossum capture success has been shown to be much higher at baited camera sites (38.96/100 trap nights) (Cove et al. 2012) when compared to sites where bait is not used (2.81/100 trap nights) (Kelly and Holub 2008) but not baiting sites is an assumption of the REM. Findings show that REM estimates may be more accurate for species that are easier to detect with camera traps and traditional mark-recapture methods may be more effective for species such as Virginia opossums. A previous camera trap study was conducted at FCJMTC in 2005 but researchers only detected two coyotes and two northern raccoons in 1,069 camera trap nights so data is insufficient for a comparison of mesopredator numbers (ARARNG 2005). Due to the high variability in sampling data it would be beneficial to increase camera trap survey effort for future studies by surveying more sites.

Animal velocity (km/day) is an important element in the REM equation because slight variations in velocity drastically change the REM estimate and can result in biased estimates. For example, a variation in coyote velocity from 12.18 km/day to 8.55 km/day changes the REM estimate from 1.62 coyotes/km^2 to 2.31 animals/km^2 (Table 1.8). The velocities selected for the REM were from studies in habitats and regions most similar to FCJMTC that collected telemetry data at short intervals (.5 to 1 hour) (Table 1.9). Ideally, animals would have been radio-collared

and tracked on FCJMTC in different habitat types to acquire more accurate velocity estimates for the REM but there were time and budget constraints. As technology advances such as GPS tracking and accelerometers become more affordable, it will be easier to collect more accurate velocity measurements. Other REM studies have used movement time of animals within the camera's detection zone to determine velocity (Rowcliffe et al. 2011). While this allows velocity estimates for each species to be estimated across each habitat type there were concerns that camera traps are noticed by individuals and alter behavior and movement patterns (Meek et al. 2016). Furthermore, for this study there were not enough mesopredator sightings to estimate speed of movement in each habitat type so velocity estimates from previous literature were used.

A 30-minute time period was used to identify independent mesopredator sightings but data from a single bottomland hardwood site in 2017 had 27 independent coyote sightings. This indicates a longer time period may be needed to identify independent sightings for certain species or an effort should be made to account for sites where there was high activity, most likely being the same individuals traveling to and from a den on multiple occasions.

Habitat Associations

Mesopredators were most abundant in the bottomland hardwood, oak, deciduous and developed habitat types (Figures 1.12 to 1.15). Virginia opossums were seen in the deciduous, oak and bottomland hardwood habitats. I expected to capture Virginia opossums in wooded areas because trees provide cover and den areas (Beatty et al. 2014). Virginia opossums often den in trees, thickets, and stump holes (Allen et al. 1985) but they can also den in brush piles and rocky outcrops and gullies (Fitch and Shirer 1970). These den types are found predominately in forested areas so it was expected to find more Virginia opossums in woodland areas. Northern raccoons were seen most often in the bottomland hardwood and oak habitats, which was

expected based on preferential selection of dens in tree cavities, ample cover and year-round availability of food resources (Beasley et al. 2007). Coyotes were found predominately in the bottomland hardwood, oak and grassland/ prairie habitats. While it was expected to find coyotes in open habitats such as grassland/ prairie, the abundance of coyotes in the bottomland hardwood was unexpected but may be accounted for due to resource availability. A 2017 study on small mammals found an abundance of rodents in the bottomland hardwood habitat, which could provide a food source for mesopredators (FTN 2017). Bobcats were seen most often in the bottomland hardwood, oak and deciduous habitat types. Small rodents are a food source for bobcats (Rolley and Warde 1985) and they have been known to hunt and rest and bottomland hardwood forests (Hall and Newsom 1978) but can be seen across many habitat types.

High ABB Zones

There was no significant difference in the number of mesopredators found inside and outside of the high ABB zone, which suggests that potential competition is not influencing distribution across FCJMTC. ABBs were not trapped at the same locations where mesopredator camera traps were placed so it is difficult to make a direct comparison between abundances. Only a small number of camera traps were encompassed in the high ABB zone, which could decrease the ability to detect a difference inside and outside of the high ABB zone so doubling camera site placement would be suggested for future studies (Figure 1.7 and 1.10).

Edge Effects

A negative relationship was found between mesopredator counts per 100 trap nights and the distance to the edge of FCJMTC, which supported the hypothesis that more mesopredators would be found closer to the base edge. Cervinka et al. (2011) found mesopredator occurrence increased as distance to the edge decreased and mesopredators have been found to be more

abundant in fragmented and edge habitats (Dijak and Thompson 2000, Andren 1992). Findings correspond to the literature but additional camera trap effort may help further describe species associations to the base edge as detectability was low for species such as Virginia opossums. More camera trap sites spread across the base would increase coverage and help provide a better picture of where species reside in relation to different habitat types and edges. Limitations in project budget and time constraints restricted camera trap effort and criteria for the REM estimates such as random camera placement limited evenly dispersed camera placement. The uniqueness of FCJMTC may have also impacted trapping rates, as the eastern portion of the base is a highly managed wildlife management area where prescribed burns are frequently carried out to restore habitat. Furthermore, military maneuvers have been shown to impact coyote movement (Gese et al. 1989) and camera traps were deployed in peak military training season so maneuvers may have influenced mesopredator activity and detection at trap sites.

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CHAPTER 1 FIGURES AND TABLES

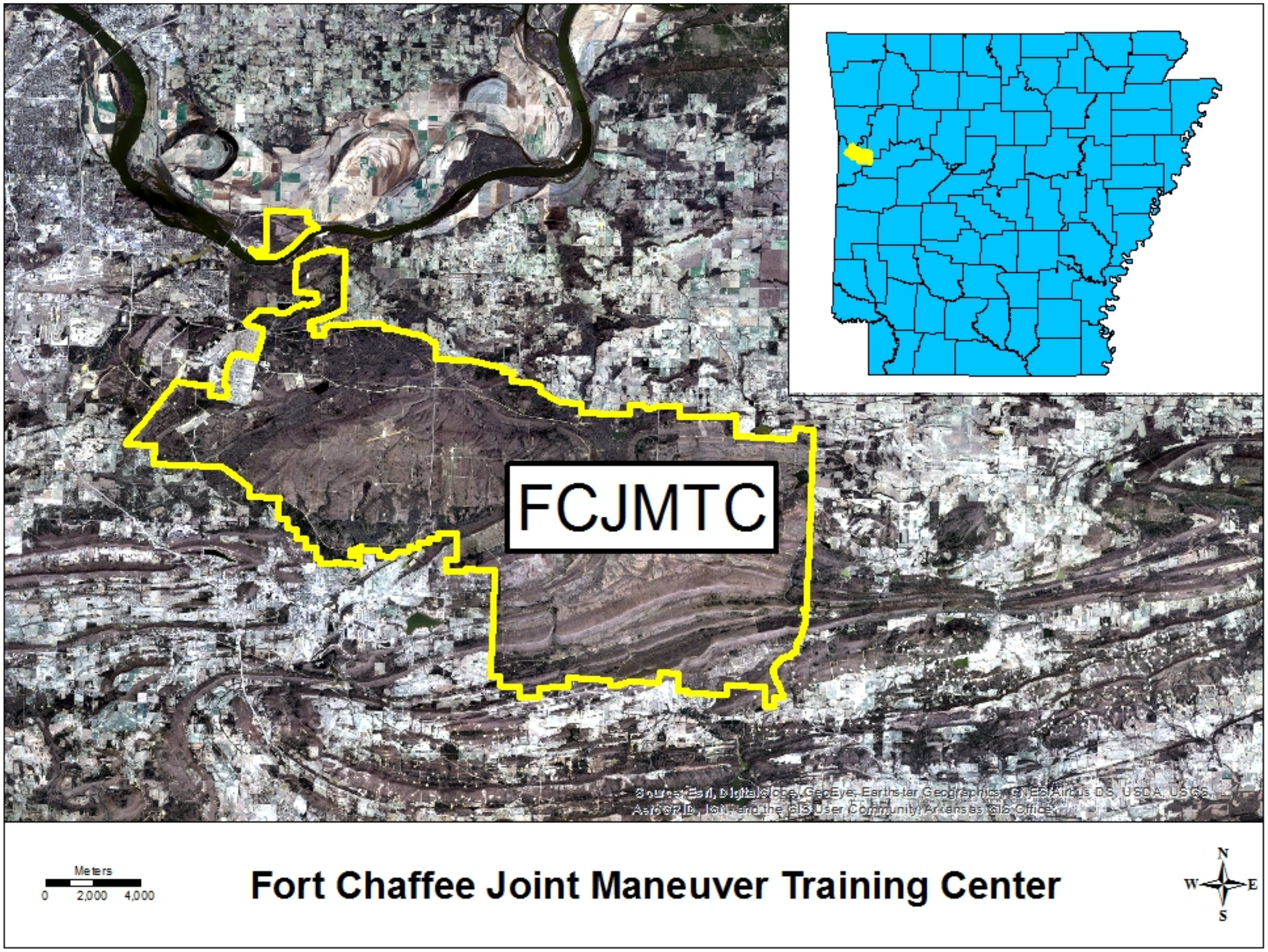

Figure 1.1. Map of the study area, FCJMTC, located primarily in the Arkansas River Valley in western Arkansas.

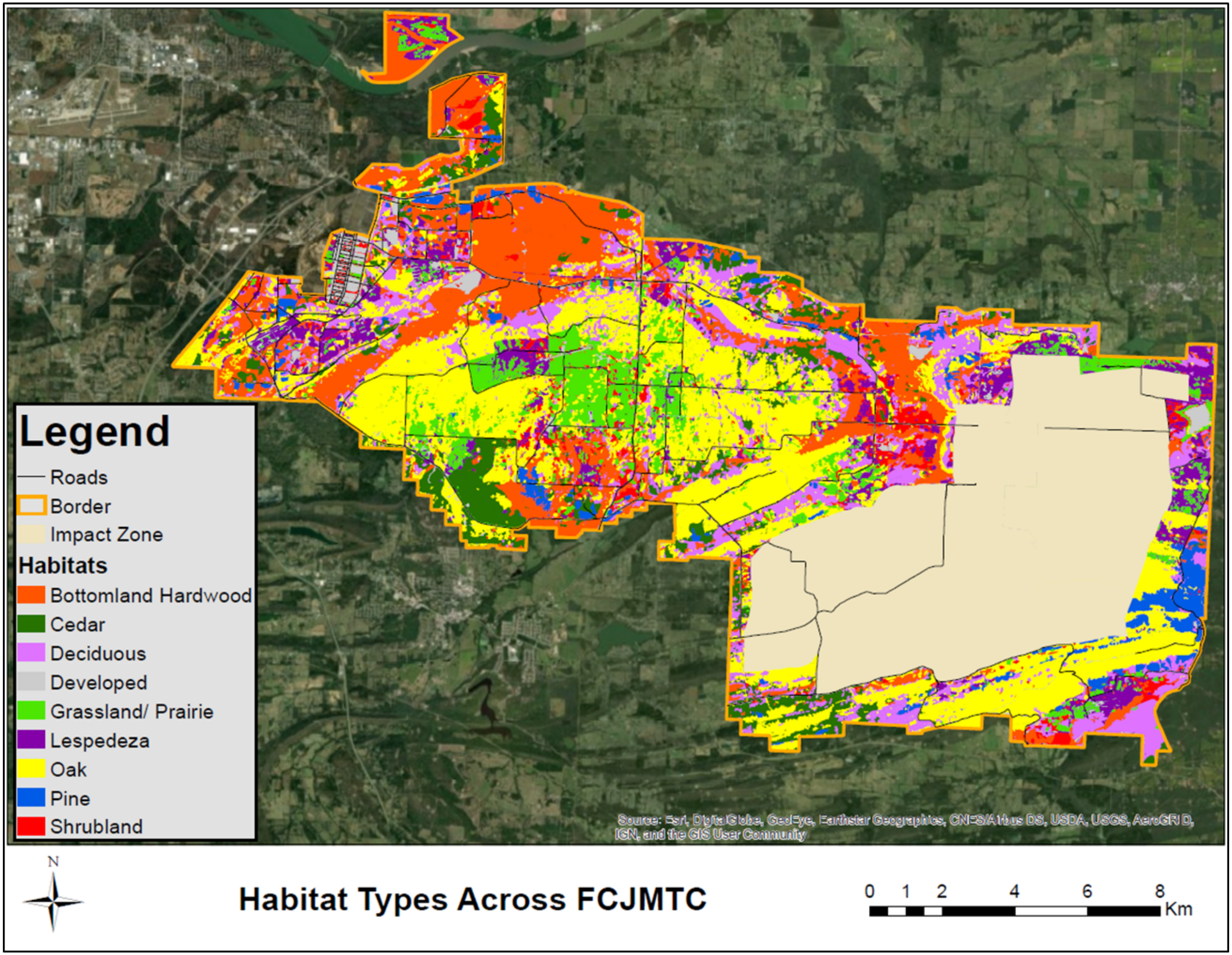

Figure 1.2. Habitat types across Fort Chaffee Joint Maneuver Training Center.

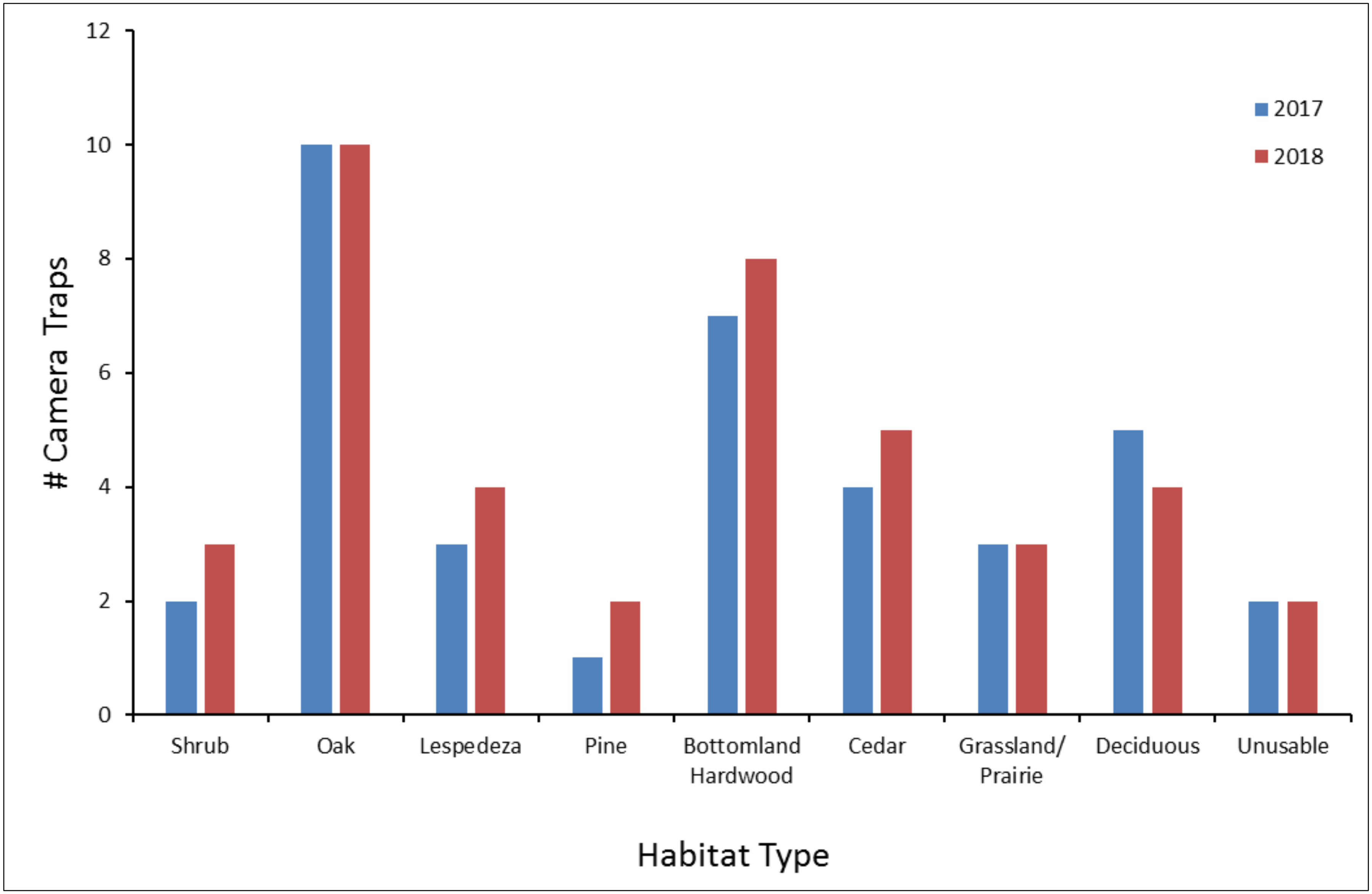

Figure 1.3. Total number of camera traps placed in each habitat type in 2017 and 2018 seasons.

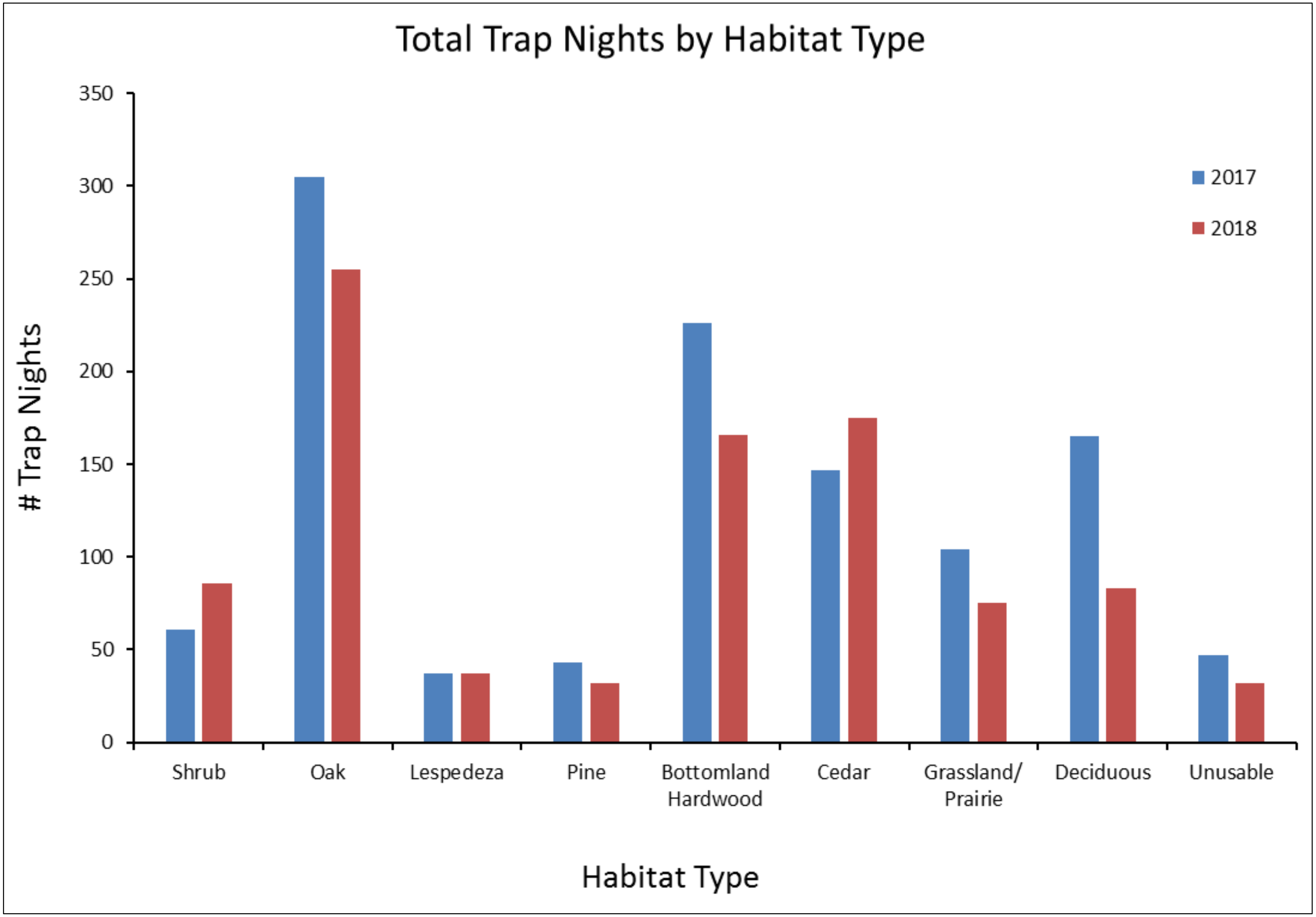

Figure 1.4. Total number of trap nights in each habitat type in 2017 and 2018 seasons.

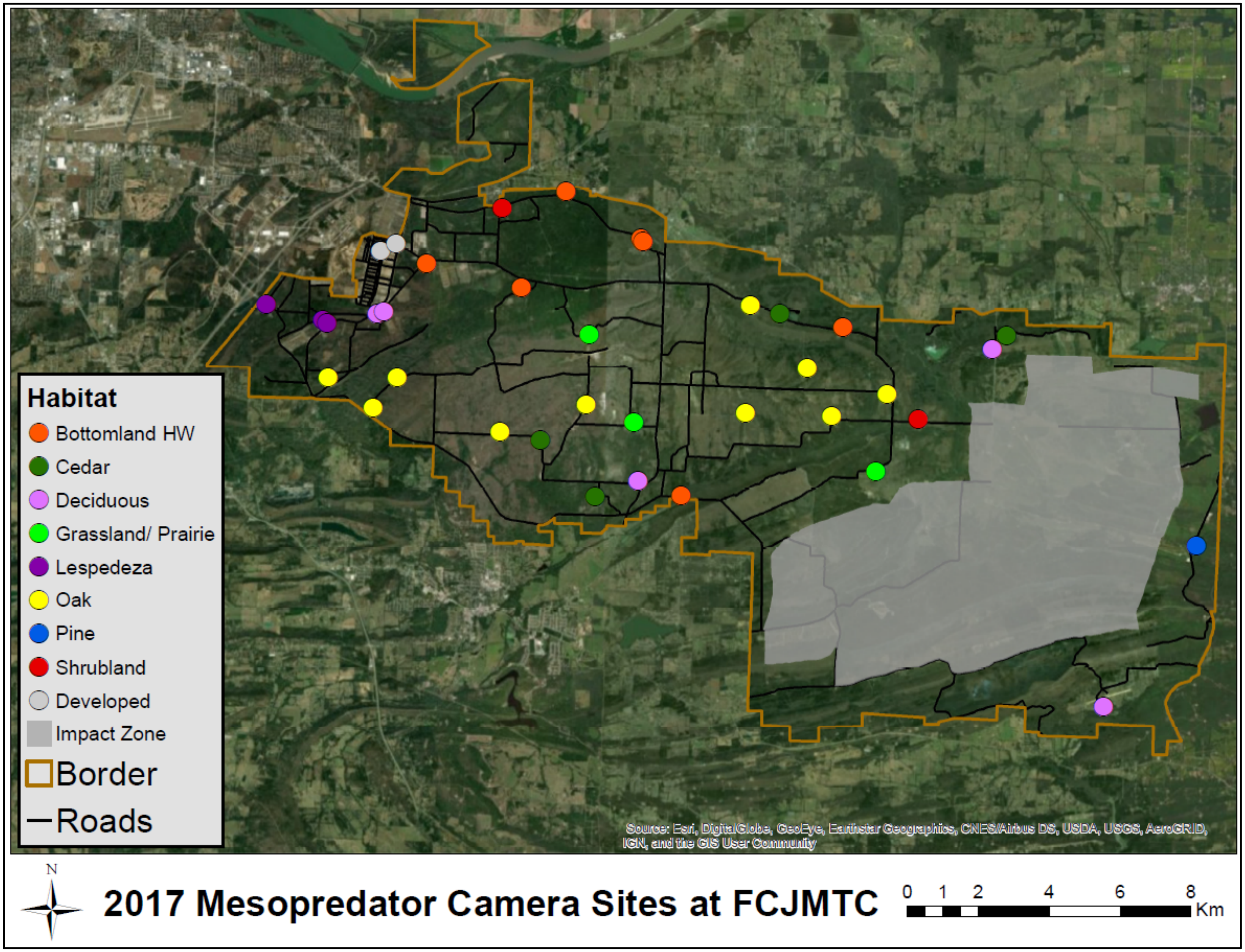

Figure 1.5. Camera trap sites by habitat type for the 2017 season.

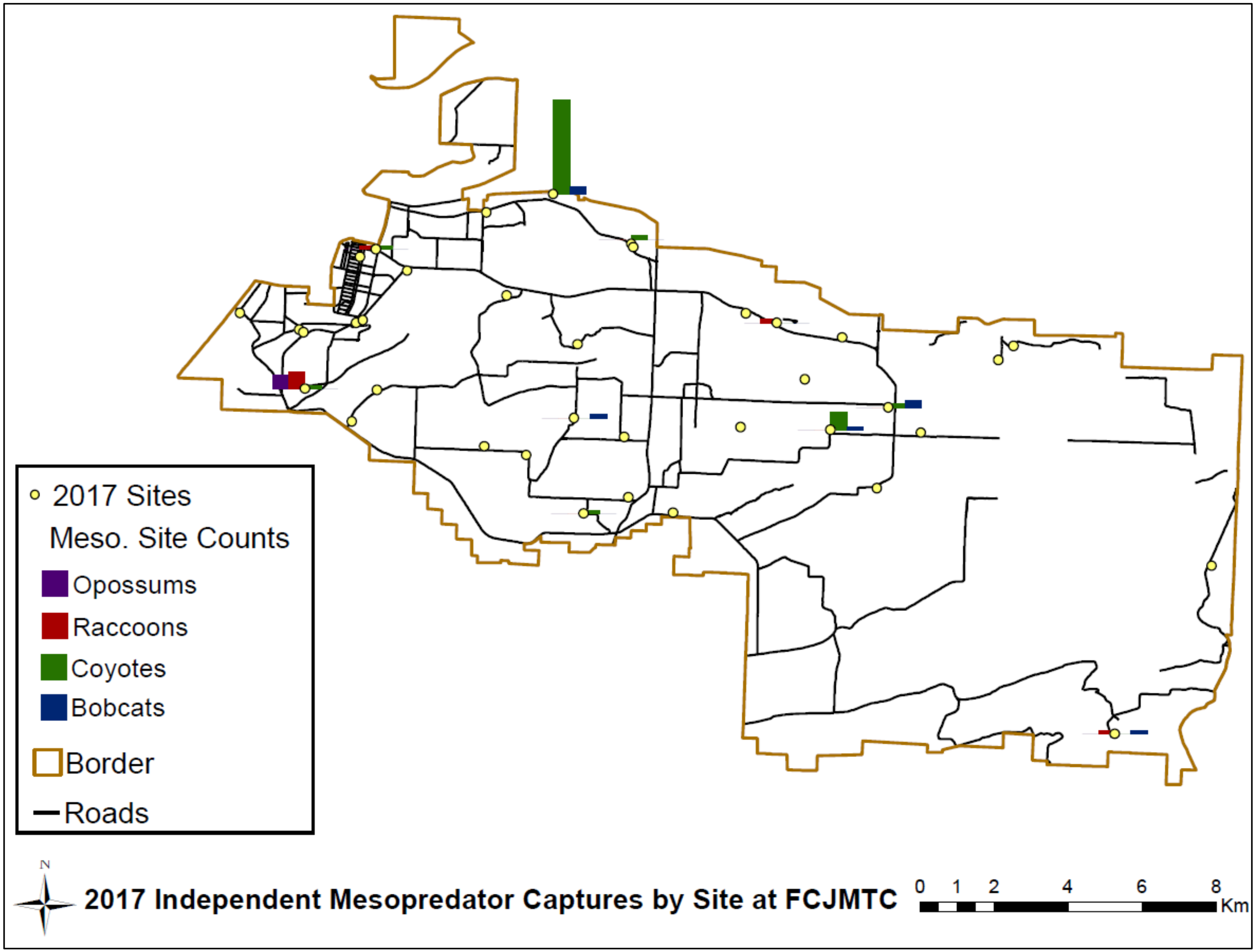

Figure 1.6. Independent mesopredator captures by camera site for the 2017 season. Values range from 0 (no bar present) to 27 (highest bar present).

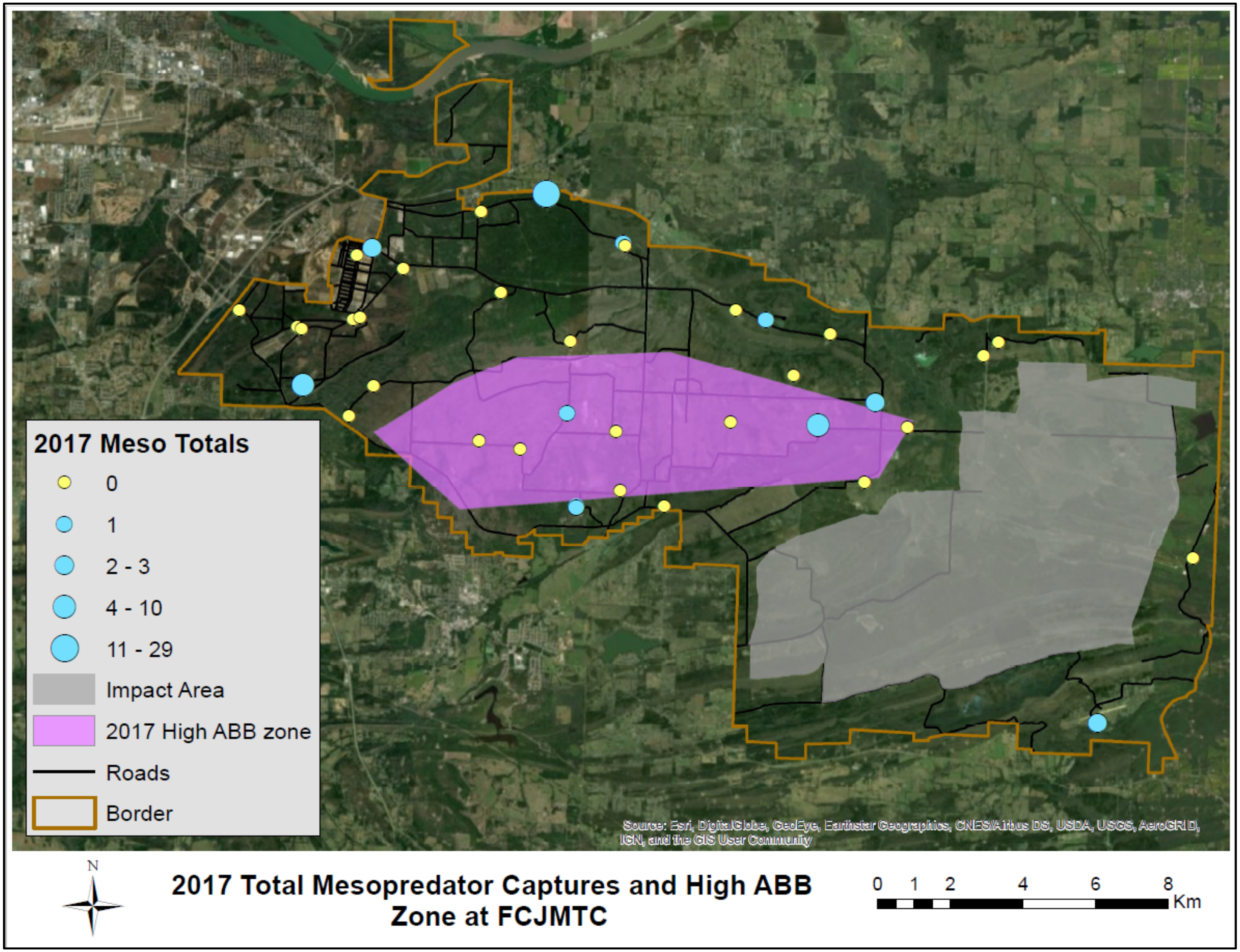

Figure 1.7. Combined mesopredator captures at each site in 2017 and overlaid 2017 high ABB zone.

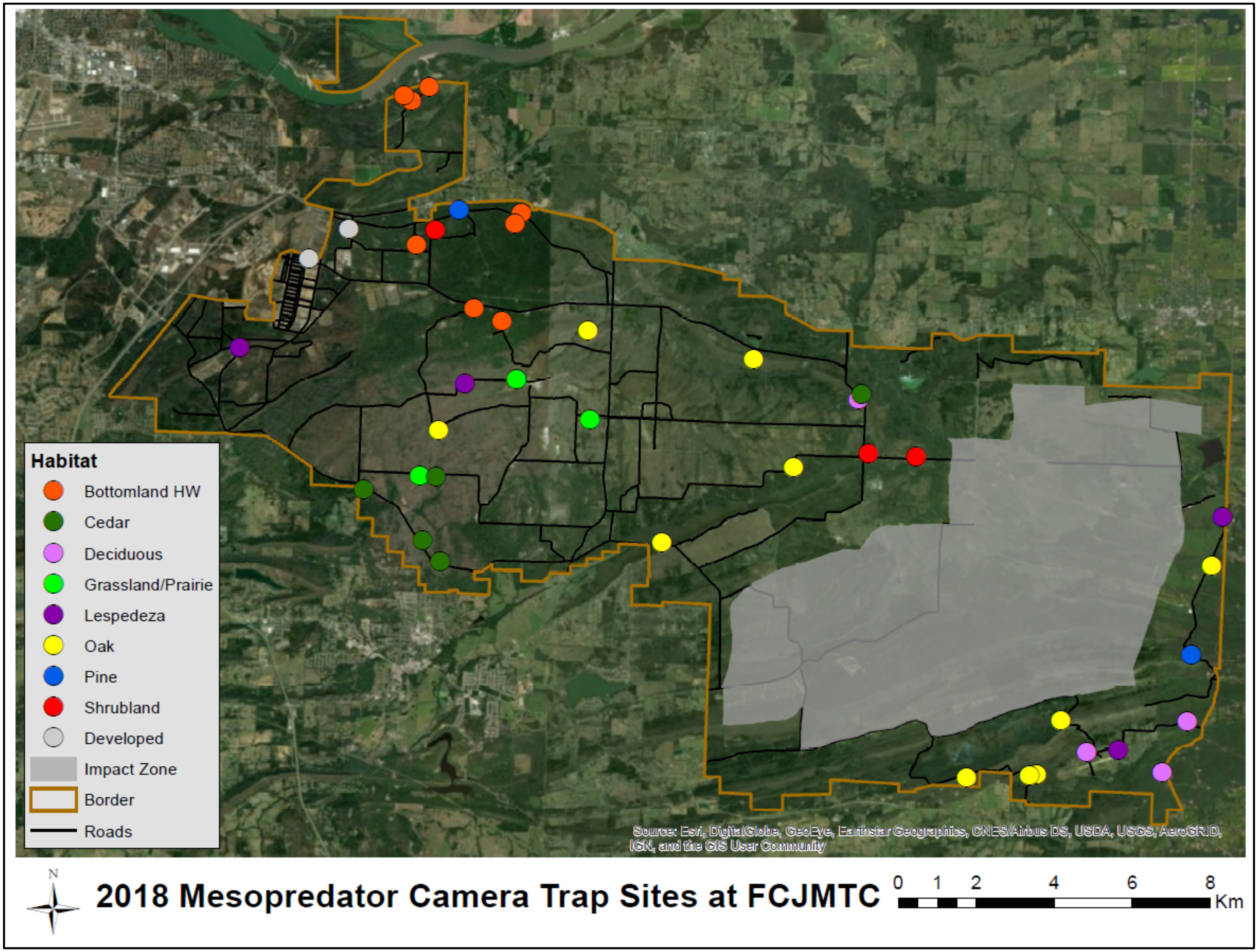

Figure 1.8. Camera trap sites by habitat type for the 2018 season.

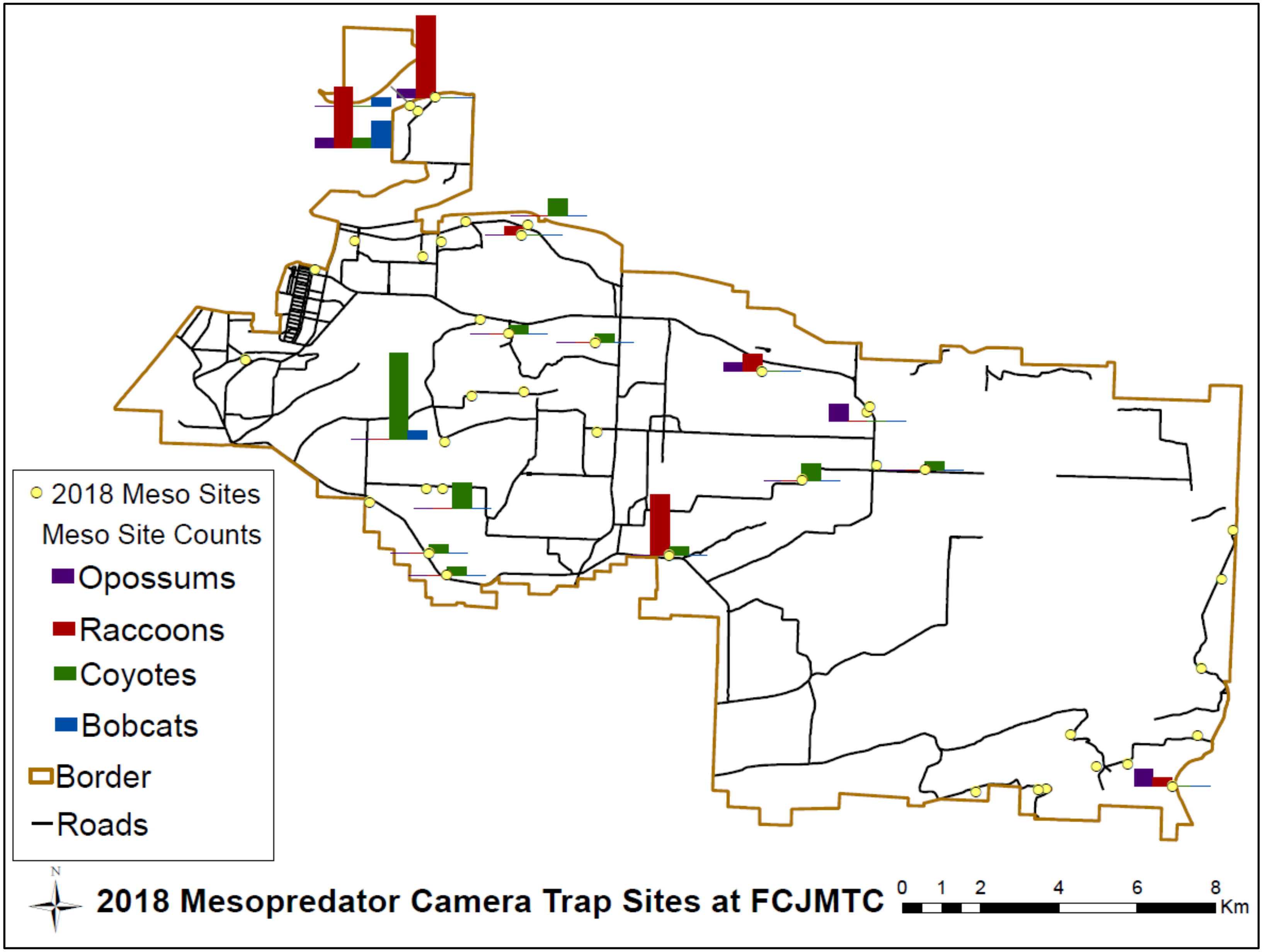

Figure 1.9. Independent mesopredator captures by camera site for the 2018 season. Values range from 0 (no bar present) to 11 (highest bar present).

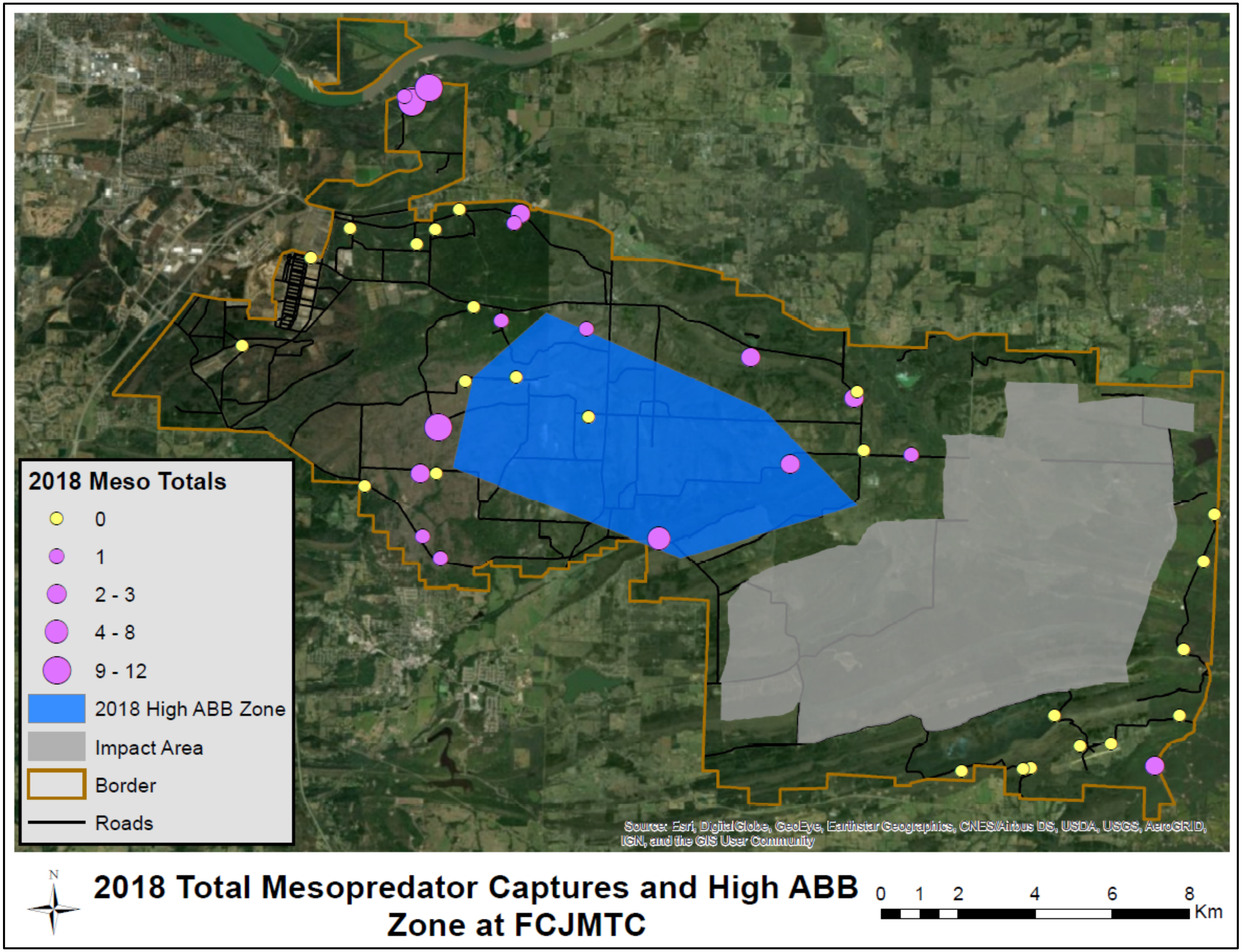

Figure 1.10. Combined mesopredator captures at each site in 2018 and overlaid 2018 high ABB zone.

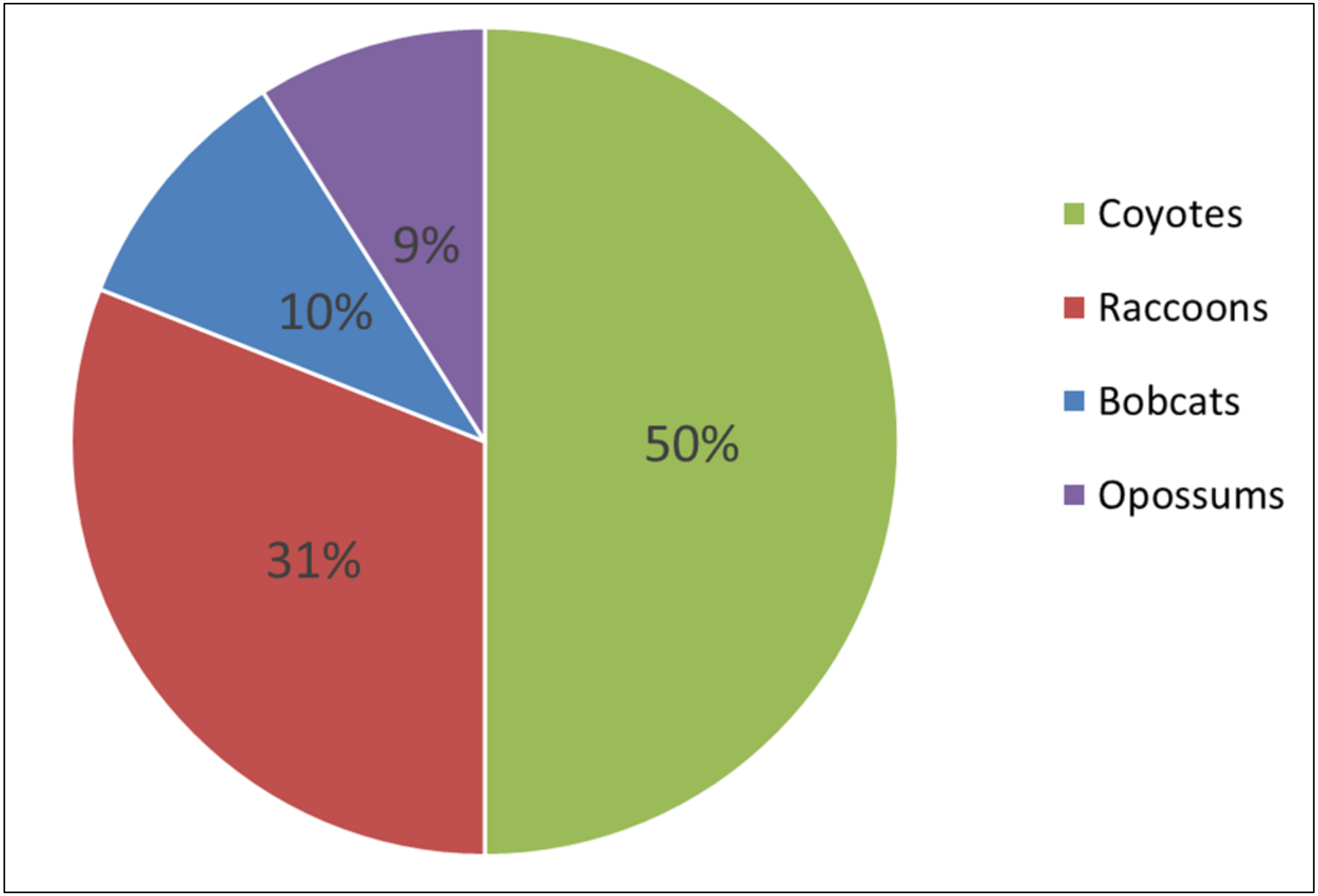

Figure 1.11. Proportion of each species of mesopredator captured during the 2017 and 2018 seasons.

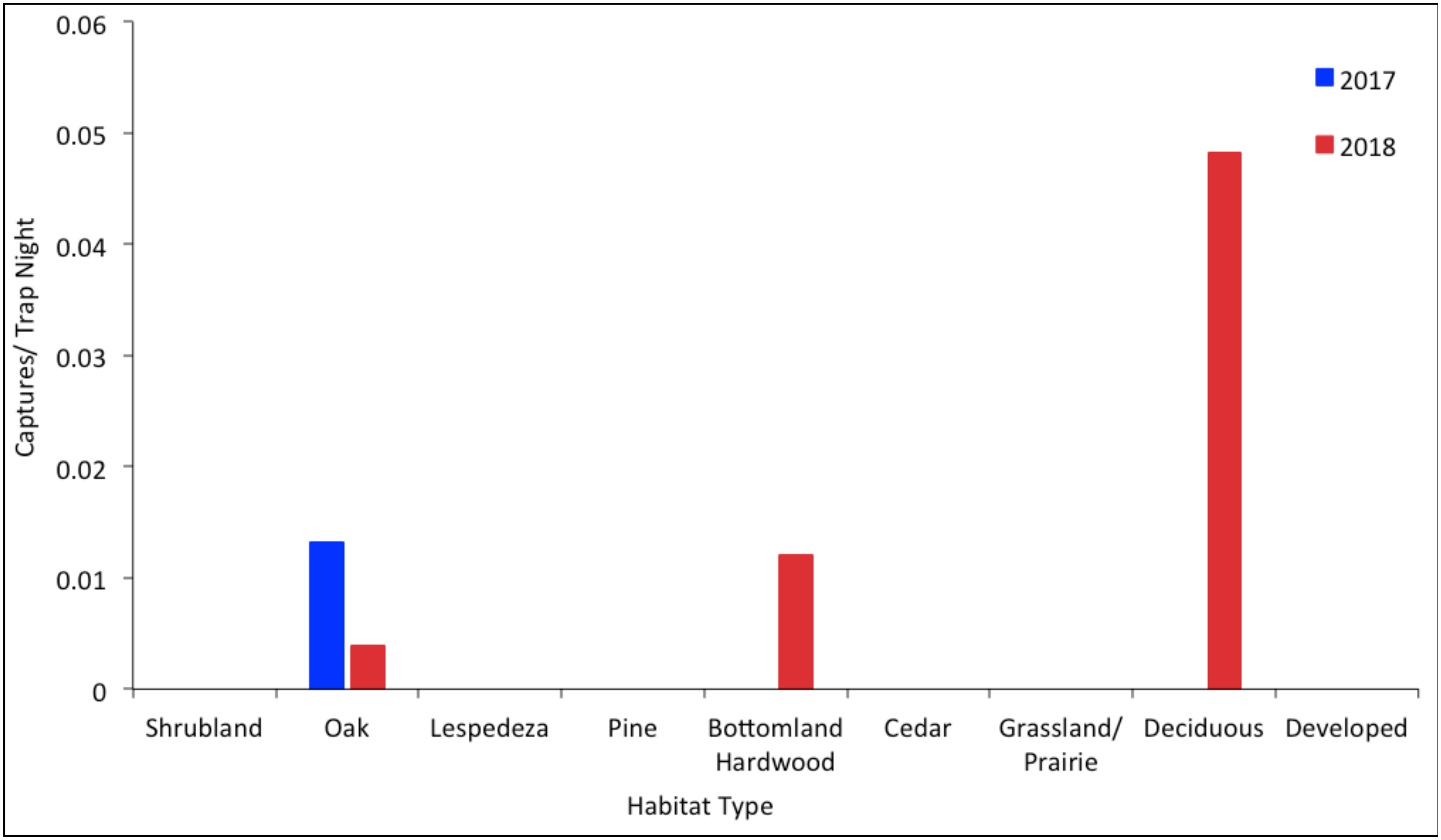

Figure 1.12. Total Virginia opossum captures per trap night by habitat type for 2017 and 2018 seasons.

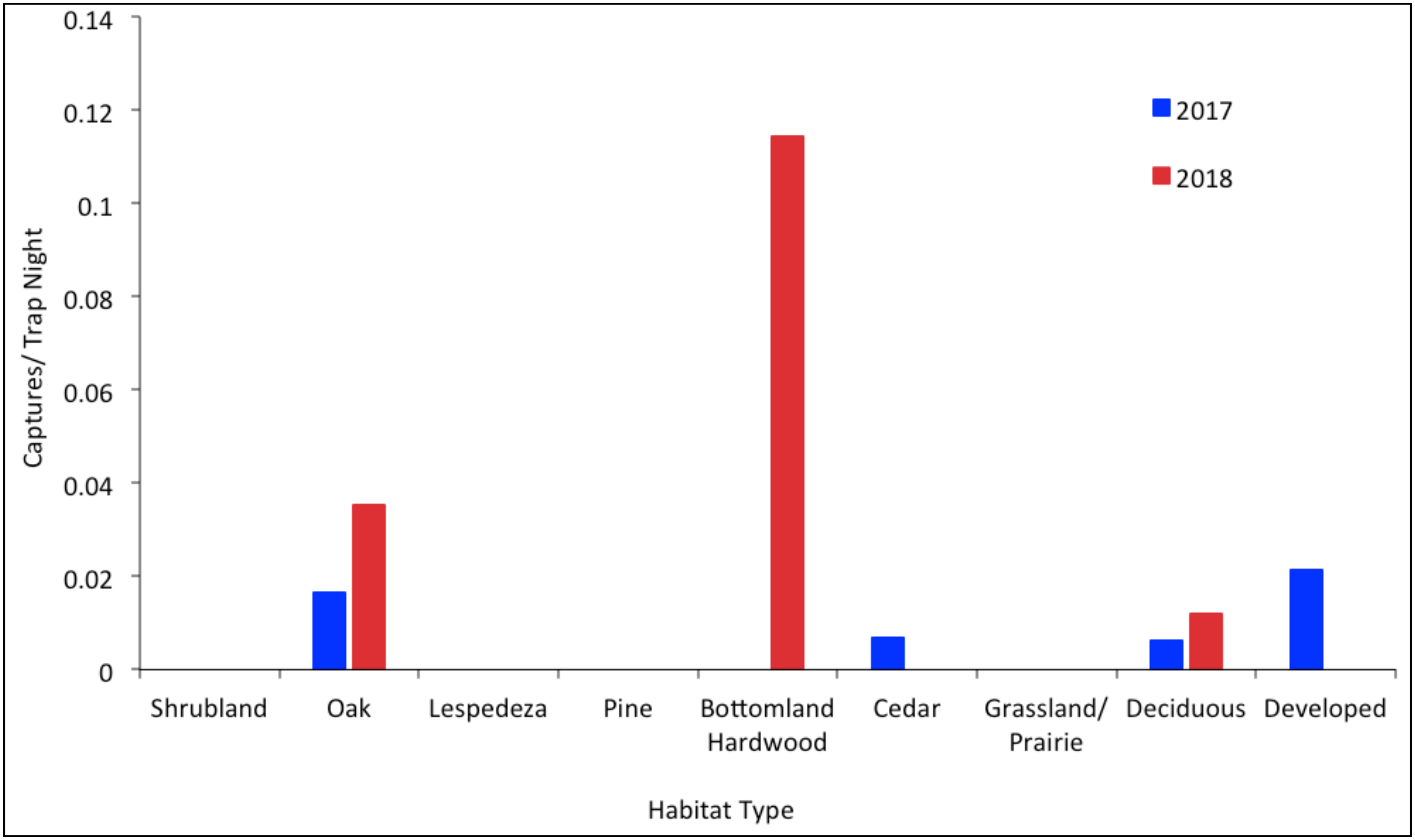

Figure 1.13. Total northern raccoon captures per trap night by habitat type for 2017 and 2018 seasons.

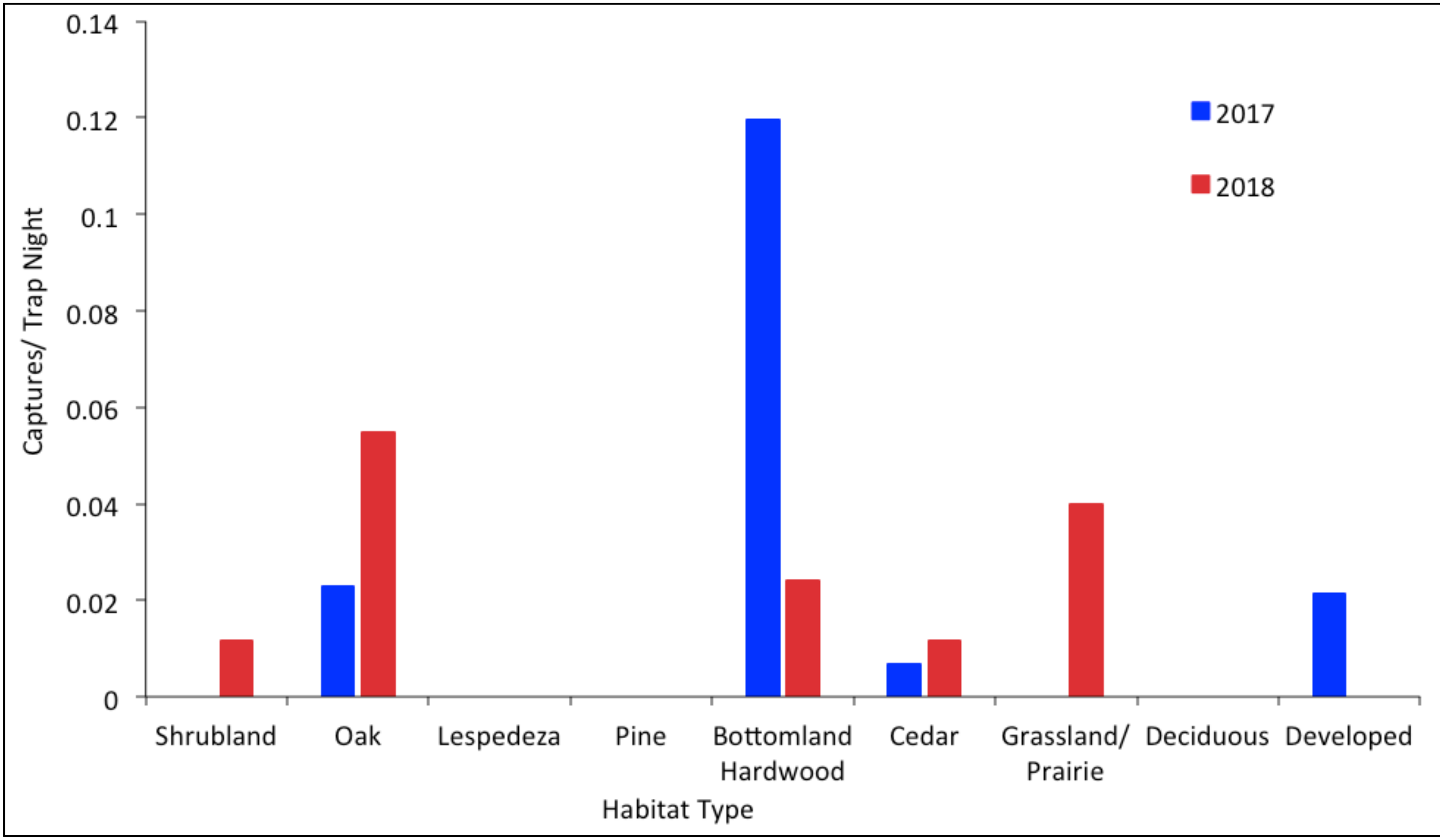

Figure 1.14. Total coyote captures per trap night by habitat type for 2017 and 2018 seasons.

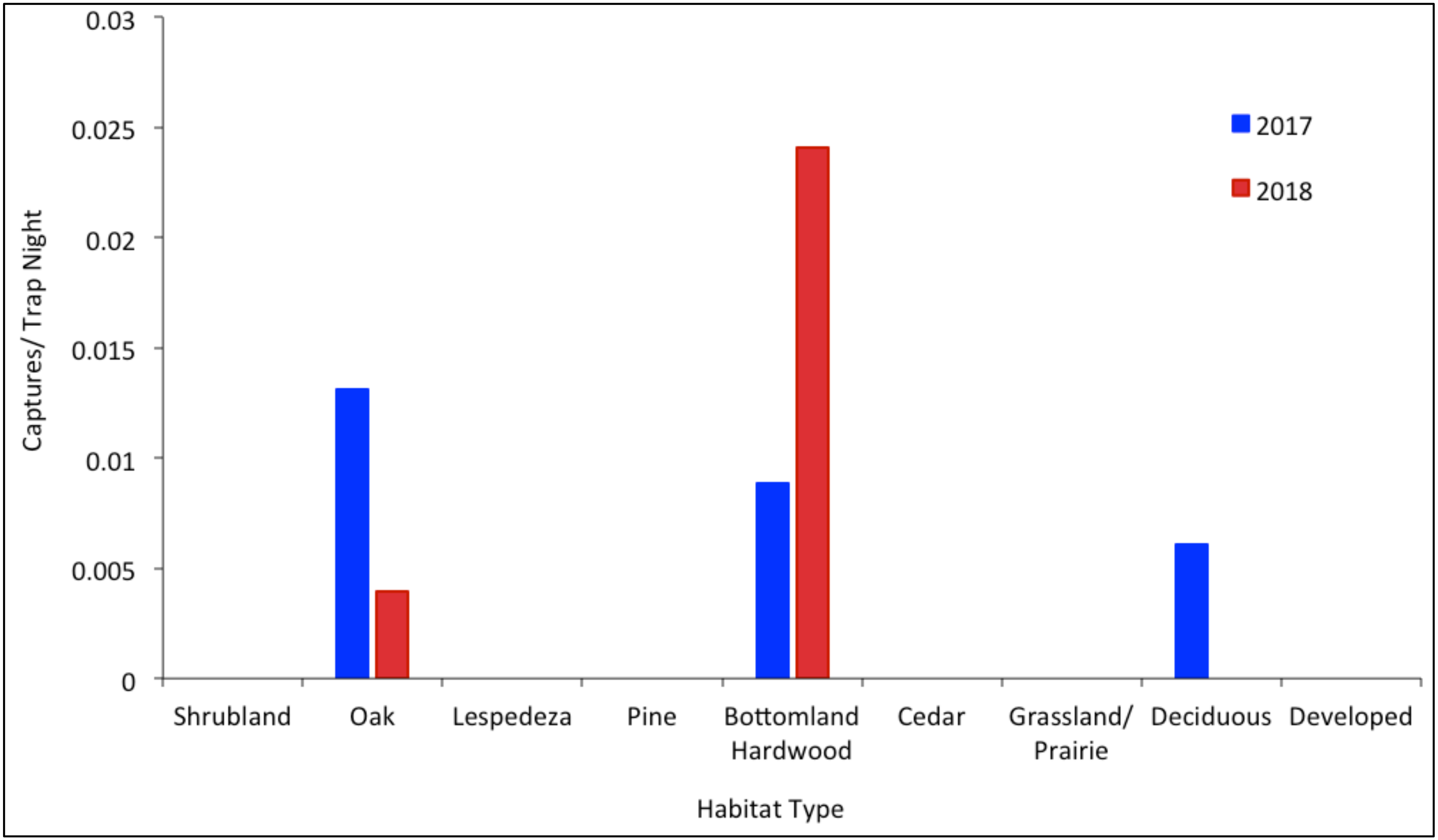

Figure 1.15. Total bobcat captures per trap night by habitat type for 2017 and 2018 seasons.

Table 1.1. Total photos captured over the two seasons at FCJMTC.

	2017	2018	Total
Total Photos	98,967	61,075	160,042
False-triggers	90,023	57,334	147,357
Total Cameras	37	41	78
Total Trap Nights	1,135	941	2,076

Table 1.2. Independent sightings of each species by season captured at FCJMTC.

Independent Sightings	2017	2018	Total
Virginia opossums	4	7	11
Northern raccoons	8	29	37
Coyotes	36	24	60
Bobcats	7	5	12
Gray Foxes	0	2	2
Pigs	48	15	63
Deer	396	398	794
Armadillos	36	28	64
House Cat	1	0	1
Chipmunk	5	1	6
Gray Squirrel	30	52	82
Eastern Cottontail	5	9	14
Rats	14	6	20
Turkey	22	17	39
Other	55	68	123
Total	667	661	1328

Table 1.3. Mesopredator REM estimates for 2017. Velocities used for each species in the REM equation were as follows: 8.55 km/day for coyotes, 2.61 km/day for northern raccoons, 7.88 km/day for bobcats and 1.10 km/day for Virginia opossums.

Habitat Type	**Number of Sites**	**Trapping Days (t)**	**Radius (km)**	**Angle (Θ)**	**Coyote Count (y)**	**Density (coyotes/ km²)**	**Raccoon Count (y)**	**Density (raccoons/ km²)**	**Bobcat Count (y)**	**Density (bobcats/km)**	**Opossum Count (y)**	**Density (opossums/l**
Shrubland	2	61	0.0057	0.38	0	0	0	0	0	0	0	0
Oak	10	305	0.0080	0.38	7	0.44	5	1.08	4	0.28	4	2.05
Lespedeza	3	37	0.0057	0.38	0	0	0	0	0	0	0	0
Pine	1	43	0.0058	0.38	0	0	0	0	0	0	0	0
Bottomland Hardwood	7	226	0.0080	0.38	27	2.31	0	0	2	0.19	0	0
Cedar	4	147	0.0058	0.38	1	0.18	1	0.67	0	0	0	0
Grassland/ Prairie	3	104	0.0057	0.38	0	0	0	0	0	0	0	0
Deciduous	5	165	0.0058	0.38	1	0.16	0	0	1	0.17	0	0
Developed	2	47	0.0058	0.38	1	0.57	1	2.10	0	0	0	0

Table 1.4. Mesopredator REM estimates for 2018. Velocities used for each species in the REM equation were as follows: 8.55 km/day for coyotes, 2.61 km/day for northern raccoons, 7.88 km/day for bobcats and 1.10 km/day for Virginia opossums.

Habitat Type	Number of Sites	Trapping Days (t)	Radius (km)	Angle (ϴ)	Coyote Count (y)	Density (coyotes/ km^2)	Raccoon Count (y)	Density (raccoons/ km^2)	Bobcat Count (y)	Density (bobcats/km)	Opossum Count (y)	Density (opossums/l
Shrubland	3	86	0.0057	0.38	1	0.31	0	0	0	0	0	0
Oak	10	255	0.0080	0.38	14	1.06	9	2.32	1	0.08	1	0.61
Lespedeza	4	37	0.0057	0.38	0	0	0	0	0	0	0	0
Pine	3	32	0.0058	0.38	0	0	0	0	0	0	0	0
Bottomland Hardwood	8	166	0.0080	0.38	4	0.47	19	7.53	4	0.51	2	1.88
Cedar	5	175	0.0058	0.38	2	0.30	0	0.00	0	0	0	0
Grassland/ Prairie	3	75	0.0057	0.38	3	1.08	0	0	0	0	0	0
Deciduous	5	83	0.0058	0.38	0	0	1	1.19	0	0	4	11.33
Developed	2	32	0.0058	0.38	0	0	0	0.00	0	0	0	0

Table 1.5. Mesopredator REM estimates for 2017 and 2018 combined data. Velocities used for each species in the REM equation were as follows: 8.55 km/day for coyotes, 2.61 km/day for northern raccoons, 7.88 km/day for bobcats and 1.10 km/day for Virginia opossums.

Habitat Type	**Number of Sites**	**Trapping Days (t)**	**Radius (km)**	**Angle (Ө)**	**Coyote Count (y)**	**Density (coyotes/ km^2)**	**Raccoon Count (y)**	**Density (raccoons/ km^2)**	**Bobcat Count (y)**	**Density (bobcats/km)**	**Opossum Count (y)**	**Density (opossums/l**
Shrubland	5	147	0.0057	0.38	1	0.18	0	0	0	0	0	0
Oak	20	560	0.0080	0.38	21	0.73	14	1.65	5	0.19	5	1.40
Lespedeza	7	74	0.0057	0.38	0	0	0	0	0	0	0	0
Pine	4	75	0.0058	0.38	0	0	0	0	0	0	0	0
Bottomland Hardwood	15	392	0.0080	0.38	31	1.53	19	3.19	6	0.32	2	0.80
Cedar	9	322	0.0058	0.38	3	0.25	1	0.31	0	0	0	0
Grassland/ Prairie	6	179	0.0057	0.38	3	0.45	0	0	0	0	0	0
Deciduous	10	248	0.0058	0.38	1	0.11	1	0.40	1	0.12	4	3.79
Developed	4	79	0.0058	0.38	1	0.34	1	1.25	0	0	0	0

Table 1.6. Program presence psi estimates by species overall in 2017 and by habitat type in 2017 at FCJMTC.

	Opossums		**Raccoons**		**Coyotes**		**Bobcats**	
	Psi (ψ)	**SE**	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**
Overall Psi (ψ)	0.028	0.028	0.158	0.017	0.229	0.079	0.276	0.162
Habitat Type	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**
Oak	0.101	0.094	0.147	0.143	0.355	0.172	0.622	0.395
Lespedeza	0	0	0	0	0	0	0	0
Shrubland	0	0	0	0	0	0	0	0
Deciduous	0	0	0.271	0.247	0	0	0.404	0.397
Pine	0	0	0	0	0	0	0	0
G/P	0	0	0	0	0	0	0	0
BHW	0	0	0	0	0.324	0.194	0.266	0.269
Cedar	0	0	0.309	0.274	0.280	0.242	0	0
Developed	0	0	1	0	1	0	0	0

Table 1.7. Program presence psi estimates by species overall in 2018 and by habitat type in 2018 at FCJMTC.

	Opossums		**Raccoons**		**Coyotes**		**Bobcats**	
	Psi (ψ)	**SE**	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**
Overall Psi (ψ)	0.208	0.113	0.153	0.058	0.462	0.139	0.106	0.066
Habitat Type	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**	**Psi (ψ)**	**SE**
Oak	0.141	0.139	0.205	0.129	0.691	0.287	0.141	0.140
Lespedeza	0	0	0	0	0	0	0	0
Shrubland	0	0	0	0	0.499	0.409	0	0
Deciduous	1	0	0.256	0.222	0	0	0	0
Pine	0	0	0	0	0	0	0	0
G/P	0	0	0	0	0.565	0.443	0	0
BHW	0.463	0.313	0.383	0.180	0.638	0.305	0.365	0.249
Cedar	0	0	0	0	0.507	0.285	0	0
Developed	0	0	0	0	0	0	0	0

Table 1.8. Example data of how REM estimates vary greatly based on changes in velocity while all other variables in the REM equation remain the same.

Habitat	Trap Days	Coyote Ind. Obs.	Velocity (km/day)	Radius (km)	Detection Angle (degrees)	REM Estimate (animals/km^2)
Bottomland Hardwood	226	27	6.15	0.00798	0.38	3.21
Bottomland Hardwood	226	27	8.55	0.00798	0.38	2.31
Bottomland Hardwood	226	27	10.9	0.00798	0.38	1.81
Bottomland Hardwood	226	27	12.18	0.00798	0.38	1.62
Bottomland Hardwood	226	27	15.14	0.00798	0.38	1.30
Bottomland Hardwood	226	27	22.56	0.00798	0.38	0.88

Table 1.9. Velocity estimates for mesopredator species taken from the literature for REM estimates.

Author	Year	State	Habitat	Species	Method	Estimate (km/day)	Intervals
Holzman et al.	1992	Georgia	Mixed	Coyote	Telemetry	8.55	1 hr
Chamberlain et al.	2003	Mississippi	Mostly forested	Bobcat	Telemetry	7.88	1 hr
Allen et al.	1985	Georgia	Mostly forested	Opossum	Telemetry	1.098	2 hr
Beasley and Rhodes	2010	Indiana	Mixed	Raccoon	Telemetry	2.61	1 hr

CHAPTER 2: EVIDENCE OF POTENTIAL COMPETITION FOR CARRION BETWEEN MESOPREDATORS AND THE ENDANGERED AMERICAN BURYING BEETLE (*NICROPHORUS AMERICANUS*) AT FORT CHAFFEE JOINT MANEUVER TRAINING CENTER

The American Burying Beetle (*Nicrophorus americanus*, hereafter ABB), once prevalent throughout the eastern part of North America has declined by as much as 90% in numbers and range (Bedick 1999). Numerous hypotheses have been suggested to explain the ABB decline following its placement on the endangered species list by the Unites States Fish and Wildlife Service (USFWS) in 1989. Hypotheses ranging from habitat loss to pesticide use and artificial lighting have been referenced (Sikes and Raithel 2002). While many of these hypotheses have been rejected, three remain that are considered the most plausible cause of the ABB decline (Kozol 1995, Anderson and Peck 1985). These hypotheses include (1) increased congener competition for carcasses, (2) decline of suitable carrion resources and (3) increased competition between vertebrate scavengers and ABBs (Sikes and Raithel 2002).

As members of the *Nicrophorus* genus, ABBs are carrion specialists and require small animal carcasses for successful reproduction (Walker 2007). A closely related congener species, *N. orbicollis*, is similar to ABBs in historic range and tolerances but in areas where it is sympatric with ABBs, it has been found to be nearly ten times more abundant (Lomolino and Creighton 1996, Amaral et al. 1997). Members of the *Nicrophorus* genus breed on carcasses ranging in size from 5-300g but ABBs prefer carcasses ranging in size from 80-100g. (Kozol et al. 1988). This narrow carcass size preference may increase resource scarcity for ABBs since appropriately-sized carcasses may be harder to find than small carcasses and because competition for carrion between ABBs, their congeners and flies (Order Diptera) increases as

carcass size increases (Schnell et al. 2008, Trumbo 1992). In addition, some potential carrion species that fall into the ideal size category for ABBs have gone extinct or declined including the passenger pigeon (*Ectopistes migratorius*) and northern bobwhite (*Colinus virginianus),* which may cause greater resource scarcity for ABB populations (Guthery et al. 2000).

Populations of ABB are currently found in Arkansas, Kansas, Massachusetts, Nebraska, Ohio, Rhode Island, South Dakota and Texas. The two largest populations are in central Nebraska and eastern Oklahoma and west-central Arkansas. Fort Chaffee Joint Maneuver Training Center (FCJMTC), a military base in western Arkansas, has the largest known population of ABBs in the state (See Figure 1.1, Chapter 1). The ABB population at FCJMTC has been surveyed annually since 1992 and trapping totals have ranged from 51 in 2012 to 851 in 2009 (FTN 2018). Yearly fluctuations are common and ABB totals from previous years indicate the population may rise and fall in cycles (FTN 2018). During my study, ABB counts were 252 and 200 for 2017 and 2018, respectively (FTN 2018). During the 2017 and 2018 ABB census, researchers found their top capture sites were all either oak woodland or grassland/ prairie habitat (FTN 2017, FTN 2018). Researchers surveyed ABBs by placing above-ground bucket traps baited with rotting chicken and one trap was placed at each site (Leasure et al. 2012).

While many of the first researchers to study ABBs hypothesized that their decline occurred because of habitat loss due to a presumed reliance on old growth forests (Anderson 1982), subsequent research has found ABBs are in fact vegetation generalists (Lomolino et al. 1995). Research has shown ABBs can be captured in different habitat types as long as the habitat contains sufficient carrion resources (Lomolino and Creighton 1996). Holloway and Schnell (1997) found a positive correlation between mammal biomass and ABB abundances at FCJMTC. ABBs were captured where there were abundant populations of small mammals regardless of

habitat type (Holloway and Schnell 1997). Creighton et al. (2007) found fewer ABBs in recently cleared sites as opposed to adjacent forested sites and suggested that while ABBs are habitat generalists, they may actively avoid disturbed sites. Although habitat alterations may not directly impact generalist ABBs, the species that serve as a carrion base for ABBs can be negatively impacted by habitat loss. Lovejoy et al. (1986) found that large rodent numbers, such as hispid cotton rats (*Sigmodon hispidus)*, which are ideally sized for ABB reproduction, decreased in disturbed habitats.

Land use changes driven by human practices have greatly altered community composition across a vast portion of the United States (Eagan et al. 2011). The vertebrate competition hypothesis implicates habitat fragmentation as an indirect cause for ABB decline due to increased densities of vertebrate scavengers in fragmented habitats. Multiple mechanisms have been proposed to explain changes in predator distribution and inflated abundance of some species in fragmented and edge habitats including: increased prey availability or diversity, ease of travel, increased foraging efficiency, and edge habitat specialization (Lidicker 1999, Lariviere 2003, Lariviere and Messier 2000, Svobodova et. al 2010). Cervinka et al. (2011) found that some mammalian mesopredators preferred edge habitat and their occurrence was negatively correlated with fragment size. Crooks (2002) showed the occurrence of Virginia opossums (*Didelphis virginiana*) and northern raccoons (*Procyon lotor*) was either unaltered or enhanced by fragmentation while coyotes and bobcats were sensitive to fragmentation and their occurrences decreased. One major consequence of habitat fragmentation is a decrease in specialist predator populations and an increase in generalist mesopredators. Specialist predator populations are often unable to survive or their populations are significantly reduced in altered or fragmented landscapes (Eagan et al. 2011). In turn, increased densities of generalist

mesopredators can negatively impact small mammal populations due to greater predation rates (Eagan et al. 2011). Crooks (2002) found apex predators such as mountain lions (*Puma concolor*), were more sensitive to fragmentation and their populations decreased as fragment size decreased while smaller species such as Virginia opossums showed the opposite effect and their numbers increased as fragment size decreased (Crooks 2002).

In addition to changes in predator communities caused by habitat fragmentation, the decline in apex predators in many ecosystems has been implicated in increased mesopredator abundances in a phenomenon known as 'mesopredator release' (Ritchie et al. 2009). A study on mesopredator release found a consistent negative relationship between coyote (*Canis latrans*) abundance, the apex predator in the studied ecosystem, and mesopredator abundance. As coyote numbers decreased the abundance of feral cats (*Felis catus*), common gray foxes (*Urocyon cinereoargenteus*), Virginia opossums, northern raccoons and striped skunks (*Mephitis mephitis*) in the area increased (Crooks and Soule 1999). Crooks and Soule (1999) also found that coyotes in the study area had an indirect positive effect on bird diversity due to a reduction in mesopredator predation (Crooks and Soule 1999). Disturbances to ecosystem balance can lead to prey redistributions and scarcity, changes in nutrient abundance and impact lower trophic level communities (Roemer 2009).

Mesopredators such as the northern raccoon, Virginia opossum, coyote, bobcat (*Lynx rufus*), gray fox and red fox (*Vulpes vulpes*) would be potential competitors for carrion within the historical distribution of ABBs. DeVault and Rhodes (2002) found 65% of brown rat (*Rattus norvegicus*) and house mouse (*Mus musculus*) carcasses were scavenged by northern raccoons, gray foxes and feral pigs (*Sus scrofa*) at their South Carolina study site. Furthermore, in a later carcass removal study, DeVault et al. (2004) found northern raccoons and Virginia opossums

removed 58% of placed carcasses, suggesting that these species may be the most likely to compete with ABBs for carrion. In a study in Nebraska's Sandhills, Jurzensky and Hoback (2011) recorded an opossum feeding on a secured rat carcass and subsequently eating seven ABBs that were also on the carcass.

In Arkansas, coyotes, bobcats, Virginia opossums and northern raccoons are commonly encountered mesopredators (Sealander and Heidt 1990). Coyotes are found across the state in Arkansas and they are especially common in western Arkansas (Sealander and Heidt 1990). They typically inhabit open habitats such as fields, shrublands and forest edges (Sealander and Heidt 1990). While there is a wide range in their diet from berries to deer carrion, their breeding success shows a close correlation with rodent availability (Sealander and Heidt 1990, Swingen et al. 2015). Years with high rodent numbers had increased breeding success suggesting small rodents are an important part of the coyote diet (Gier 1968). Bobcats are found statewide in Arkansas and they are found in many habitats from bottomland forests to grasslands but they show a preference for rocky outcrops and mature timber stands (Sealander and Heidt 1990, Rucker et al. 1989). They feed predominantly on rabbits, and small rodents but they will feed on deer carrion when it is available (Sealander and Heidt 1990). Virginia opossums are common across Arkansas and they inhabit woodland areas with a preference for bottomland forests (Sealander and Heidt 1990). They are omnivorous, opportunistic foragers. (Sealander and Heidt 1990). Northern raccoons are common across Arkansas and while they prefer bottomland hardwood habitats they are found in a variety of woodland and farmland habitats (Sealander and Heidt 1990). They are omnivorous, opportunistic foragers with diets ranging from acorns to insects and small mammals and they have adapted well to living in urban areas (Sealander and Heidt 1990). Apex predators including mountain lions and black bears (*Ursus americanus*) were

once found statewide in Arkansas but their numbers have been drastically reduced due to habitat loss (Sealander and Heidt 1990).

All of the above-mentioned mesopredators could be expected to occur at FCJMTC, however their abundances and specific habitat associations are unknown. A variety of habitat types occur on the base including: cedar, pine, oak, shrub land, developed, deciduous, grassland/ prairie, lespedeza and bottomland hardwood. Farmland, roads and urban sprawl surround the border of the military base and these anthropogenic habitat disturbances may lead to higher densities for certain mesopredator species such as Virginia opossums and northern raccoons around the base edges (Crooks 2002). While studies have been conducted on carcass removal by vertebrate scavengers as well as addressed hypotheses for the ABB decline, few studies have looked at ABBs and carrion competitors' abundances in locations where ABBs are present.

The use of camera traps in wildlife studies is a growing field that is often less costly and time consuming than traditional trapping/ tracking methods and equally or more effective (Nielsen and Cooper 2012). Camera traps allow animals to be easily identified to species and can be used over long periods of time for 24 hours a day to increase survey effort with minimal effort. FCJMTC provides a unique opportunity to study mesopredator abundance and habitat selection in a location where ABB are currently found.

Objectives:

1. Place cameras on ABB traps to examine the likelihood of competition between mesopredators and ABB for carrion resources.
2. Determine if ABB relative abundances are related to relative abundances of mesopredators.

3. Assess if mesopredator relative abundances at FCJMTC changes in relation to distance from the base edge.

I hypothesize that there will be a negative relationship between ABB numbers and mesopredator numbers due to the competition for carrion resources. I hypothesize that habitats with increased mesopredator activity will have lower ABB abundances because there will be more competition for carcasses. Specifically, I hypothesize that the bottomland hardwood habitat will have low ABB abundances, as this is a preferred habitat of northern raccoons and Virginia opossums. Also, I hypothesize that ABB traps near the edge of the base will have lower ABB abundance and increased mesopredator activity.

METHODS

Study Site

I conducted this study at FCJMTC in central-western Arkansas. FCJMTC consists of approximately 25,090 hectares (261 km^2) located primarily within the Arkansas River Valley ecoregion just east of Fort Smith in Sebastian, Crawford, and Franklin Counties. Extreme southern portions of the FCJMTC land base are located within the Ouachita Mountain ecoregion. I sampled nine different habitat types at FCJMTC including: cedar, pine, oak, shrubland, developed, deciduous, grassland/ prairie, lespedeza and bottomland hardwood. The largest portion of FCJMTC is comprised by the oak habitat at 29%, followed by 19.5% bottomland hardwood, 13% deciduous, 9% cedar, 8% lespedeza, 7.5% grassland/ prairie, 5.5% shrubland, 5% developed/ water features and 3.5% pine (See Figure 1.2, Chapter 1). The habitats, which are of varying patch sizes, are spread across FCJMTC. Average rainfall at FCJMTC is 107 cm and May and June generally see the most rainfall (Cox et al. 1975). In 2017, the highest temperature in the area was 37 °C in July and the highest mean monthly temperature was 34.1 °C in July. The

lowest temperature was -14.4 °C in January and the lowest mean monthly temperature was 0.94 °C (SERCC 2017). A variety of soil types exist which exhibit a varied distribution at FCJMTC from 3 to 35% clay to 15 to 75% sand and 20 to 65% silt (Lomolino et al.1995).

Camera Traps

In order to assess the likelihood of mesopredator competition for carcasses, I placed camera traps facing ABB traps, 3-6 m from the traps on either a nearby tree or on a post. The camera traps were used in conjunction with the yearly ABB census over the two summers (2017-2018) to determine what mesopredators came in to contact with the baited ABB traps. The ABB bucket trap survey occurred from August 1-6 in 2017 and August 6-12 in 2018. Camera traps were placed on 37 of 59 ABB traps in 2017 and 35 of 63 ABB traps in 2018. Camera trap locations spanned a range of ABB captures in previous years, in a variety of habitat types (Figure 2.1). Oak habitat was the dominant habitat type at FCJMTC and therefore received the most camera traps (20), while pine habitat was the least common and received only 2 camera traps (Figure 2.1). Directly surveying the ABB traps removed any uncertainty regarding surveying at a different time of year due to varying weather conditions or putting ABBs at risk by placing additional carrion in the field.

Cameras traps have been found to be a successful tool for detecting mesopredators, as well as other mammal species (Cove et al. 2012). I used Spypoint Force® 10 cameras that operated 24 hours a day and used a passive infrared sensor (PIR) to trigger the camera to take photos. The PIR sensor was able to detect IR radiation that was emitted from objects passing through the camera's detection zone. The sensor could detect an object's surface temperature and rapid temperature changes caused the pyroelectric elements in the sensor to produce a current that triggered the camera (Welbourne et al. 2016). In a thermally heterogeneous environment,

objects moving in the background, such as branches swaying in the wind, could cause false-triggers. The air temperature had no effect on the passive infrared sensors and the sensors could detect both increases and decreases in temperature (Welbourne et al. 2016). The cameras had a 0.32 second trigger speed with a 0.52 s recovery time between pictures, an up to 24 m detection range and 42 LEDs for nighttime illumination.

To determine mesopredator relative abundance at ABB traps, I counted the number of animals photographed by the camera traps and recorded species to the best of my ability as well as time and location of the photograph. Individuals that were unable to be identified to species were placed in a category called other. In order to avoid counting an animal twice, if it was clear the animal was present in subsequent frames it was only recorded once and if the same species was seen at one location within a period of 30 minutes it was excluded to ensure events were independent (Tobler et al. 2008). To assess if habitat fragmentation impacts mesopredator and ABB abundances I looked at the distance from the trap to the edge of FCJMTC. I used ArcGIS version 10.3.1 (ESRI) to create a map of Fort Chaffee and then overlaid a vegetation map to determine what habitat type was surrounding each ABB trap. The near tool in ArcGIS was used to determine the distance from each trap location to the edge of the base. A base map of FCJMTC, a detailed vegetation map and the exact location of each ABB trap were provided by FTN Associates Ltd. biologists. ABBs were counted each morning by FTN representatives and data was taken from their yearly reports for this study. In order to assess if there was overlap between ABB and mesopredator ranges on FCJMTC a high ABB zone convex polygon that connected the ABB sites with ABB captures higher than the mean was generated in ArcGIS using the minimum bounding geometry data management tool. A polygon was created for both 2017 and 2018 seasons.

Data Analysis

I ran a Shapiro-Wilk Test to determine if data met the assumptions for normality as well as inspection of plots. A negative binomial regression was run between total mesopredator counts and ABB counts due to the lack of normality, abundance of zeros due to no mesopredator captures, and overdispersion. The level of significance was set at 0.05 for all tests. The cooccur package in RStudio was run to investigate significant pair-wise patterns of co-occurrence between mesopredators and ABBs from presence/ absence data at each camera site. The threshold was set to true for the cooccur package to summarize the important species associations as suggested by Veech (2013) and Griffith et al. (2016). A high ABB polygon was generated from ABB census data and a Wilcoxon Rank Sum test was conducted between sites inside and outside the high ABB zone. A negative binomial was conducted to evaluate if a relationship existed between mesopredator abundances and distance to the edge of FCJMTC due to the lack of normality, overdispersion and an abundance of zeros due to sites without mesopredator captures.

RESULTS

Mesopredator Abundances at ABB Traps

I captured 56 independent animal sightings in 2017 over 111 trap nights and 61 independent animal sightings in 2018 over 105 trap nights (Table 2.1 and 2.2). Over the two seasons I collected 48,998 photos at 72 camera sites in nine habitat types and 41,072 of those were false-triggers, meaning something other than an animal, such as leaves moving in the wind, triggered the camera (Table 2.1). I collected pictures of over 10 different species and overall Virginia opossums had the most sightings. Of these species, commonly captured mesopredators included Virginia opossums, northern raccoons, coyotes and bobcats. Overall, these

mesopredators made up 55% of 117 independent animal sightings (Table 2.2). Virginia opossums were the most captured mesopredator at 48 (75%) independent sightings followed by northern raccoons, coyotes and bobcats at 9 (14%), 4 (6%) and 3 (5%) independent sightings respectively (Figure 2.3 and Table 2.2).

The most ABBs were captured per trap in the grassland prairie, oak, lespedeza and shrubland habitats (Figure 2.2). In 2017, 210 ABBs were captured at the 37 trap sites monitored for mesopredators and 154 ABBs were captured at the 35 trap sites monitored for mesopredators in 2018 (Table 2.1, Figure 2.5 and Figure 2.9). Over the two seasons, Virginia opossums had the highest number of captures per trap in the pine, developed and shrubland habitats (Figure 2.4, Figure 2.6 and Figure 2.10). Northern raccoons had the highest number of captures per trap in the bottomland hardwood and cedar habitats. Coyote numbers were highest in per camera trap in the grassland/ prairie habitat and bobcats were only seen in the grassland/ prairie habitat (Figure 2.4).

ABB and Mesopredator Site Comparison

For the 2017 season, there was no significant relationship between ABB and mesopredators counts (estimate = -0.18, SE = 0.19, $p = 0.34$). For the 2018 season, there was a negative relationship between ABB and mesopredator counts (estimate = -0.66, SE = 0.22, $p<0.01$). When the seasons were combined, there was a negative relationship between ABB and mesopredator counts (estimate = -0.34, SE = 0.14, $p<0.05$).

Co-occurrence

There were no statistically significant co-occurrence patterns between any of the input species (Virginia opossums, northern raccoons, coyotes, bobcats and ABBs) in 2017 or 2018 ($p>0.05$ for all combinations). However, the p-value in 2018 was nearly significant ($p = 0.057$)

for the Virginia opossum and ABB pairing showing they co-occurred less than expected. In addition, when the seasons were combined the p-value was nearly significant for the Virginia opossum and ABB pairing ($p = 0.089$), and the northern raccoon and ABB pairing ($p = 0.051$)

High Density ABB Area

Mean ABB captures per site was 5.7 in 2017 and 4.4 in 2018. The Shapiro-Wilk Test indicated the assumption of normality was not met in 2017 ($W=0.661$, $p<0.001$) or 2018 ($W=0.733$, $p<0.001$). No significant difference was found between mesopredator captures inside and outside the high ABB zone in 2017 ($W=152.5$, $p=0.602$) (Figure 2.7) but in 2018 there were significantly more mesopredator captures outside of the high ABB area ($W=55.5$, $p<0.001$) (Figure 2.11). Overall, when 2017 and 2018 are combined there were significantly more mesopredator captures outside of the ABB areas in comparison to within the high ABB areas ($W=409$, $P<0.01$).

Edge Effects

In 2017, the negative binomial regression showed there was no relationship between mesopredator counts and distance to the edge of the base (estimate = -0.0002, SE = 0.0002, $p = 0.27$). In 2018, there was a negative relationship and mesopredator counts decreased as distance to the edge of the base increased (estimate = -0.0006, SE = 0.0002, $p < 0.01$). When the seasons were combined, there was a negative relationship and mesopredator counts decreased as distance to the edge of the base increased (estimate = -0.0004, SE = 0.0002, $p < 0.01$).

DISCUSSION

Relative Abundances

My cooccur data suggested that presence of ABBs was negatively associated with Virginia opossum and northern raccoon occurrence across ABB capture sites. ABBs may have

been avoiding sites that had high mesopredator abundances to avoid competition for carrion resources. Virginia opossums were the most abundant mesopredators captured at ABB traps followed by northern raccoons. If there was competition for carrion between mesopredators and ABBs, Virginia opossums and northern raccoons likely would be the top competitors. In fact, carcass removal studies have found Virginia opossums and northern raccoons were among the most common mammalian scavengers (DeVault et al. 2004, DeVault and Rhodes 2002, Turner et al. 2017). I detected more mesopredators outside of the high ABB zone when both seasons were combined, which supports the hypothesis that there is competition for carrion and that this may be a contributing factor in the ABB decline. Results for 2017 did not show significantly more mesopredators outside of the ABB zone but the 2017 zone also had two high capture sites that were distant from the main high capture grouping and encompassed six sites with lower than average captures (Figure 2.8). On the other hand, in 2018 the high ABB sites were closely grouped and only two sites with lower than average captures were encompassed by the high ABB zone convex polygon (Figure 2.12). As mesopredator numbers increased, ABB numbers decreased when compared by site over the two seasons, which may be a result of competition between the species for carrion.

Habitat Associations

ABBs were found in the central, interior area of FCJMTC, consistent with previous surveys (FTN 2016), while higher numbers of mesopredators were captured outside of the high ABB zone near the edges of the base. ABBs were predominately captured in grassland/ prairie, oak, lespedeza and grassland habitats. Virginia opossums and northern raccoons were predominately captured in pine, developed, shrubland and bottomland hardwood habitats. Consistent with my observations, Turner et al. (2017) found rat carcasses were scavenged by

vertebrates most often in immature pine forests (68.4%), followed by hardwoods (52.2%), and clearcuts (45.8%). In contrast, ABBs were found most often in open areas and least often in dense hardwood habitats, which further supports the hypothesis that ABBs were avoiding areas where vertebrate competition for carrion was high. While my results suggest that competition for carrion resources may influence the location of ABBs, habitat type could also play an important role. Mesopredators and ABBs may prefer certain habitat types or spatial locations on the base that lead to variations in distribution. Further research should be conducted to identify additional influential factors. More mesopredators were also seen as distance to the edge of the base decreased, which was expected based on previous fragmented landscape and edge habitat literature (Lidicker 1999, Lariviere 2003, Lariviere and Messier 2000, Svobodova et. al 2010).

Future Considerations

No prior mesopredator numbers are available to compare study results to assess mesopredator release. A previous camera trap study was conducted at FCJMTC in 2005 but researchers only detected two coyotes and two northern raccoons in 1,069 camera trap nights so data is insufficient for a comparison of mesopredator numbers (ARARNG 2005). While placing carcasses out and determining what species approached and removed them and when would be optimal for studying direct competition, the USFWS regulations prohibits testing situations that could potentially interfere with an endangered species.

Studying carcass detection time could lead to a better understanding of competition between ABBs and mesopredators. Jurzenski and Hoback (2011) found Virginia opossums not only competed with ABB for carcasses but also directly fed on ABBs that were on carcasses. Turner et al. (2017) suggested carcass size, season and habitat attributes all influence carrion acquisition by vertebrate scavengers. Turner et al. (2017) found a positive relationship between

carcass size and vertebrate scavenger success. ABBs preference for larger carcasses (80-100g as opposed to other *Nicrophorus spp.* that can use 5g carcasses) may be a contributing factor in their decline while other *Nicrophorus spp.* remain abundant. Prior studies have looked at carcass removal time by vertebrate scavengers but monitoring carcasses for ABB activity could reveal which species are able to detect and utilize carcasses first in different habitat types. I used rotten chicken as bait in the ABB traps and while this attracted both ABBs and vertebrate scavengers the carcass type can impact scavengers. Olsen et al. (2016) found that the carcass type affected what species fed on it. For example, Virginia opossums fed on northern raccoon, rabbit and Virginia opossum carcasses while northern raccoons predominately fed on rabbit carcasses. Turner et al. (2017) also found that pig carcasses were scavenged more often (98%) than rabbit (79%) and rat (54%). While rotting chicken was effective at attracting mesopredators and ABBs, it may attract a different range of species than a carcass, such as a hispid cotton rat that is optimal for ABB reproduction, would attract. A minimal number of cameras in certain habitat types may have inflated capture numbers by chance if the camera happened to be in a high activity site so more camera sites could provide a more complete picture. Increasing trapping effort for future studies is recommended but time and budget constraints limited effort for this study.

My results supported the carcass competition hypothesis at FCJMTC. It is possible that the phenomenon of mesopredator release has led to increased competition between mesopredators and ABBs and contributed to ABB extirpation in locations across the eastern United States. FCJMTC is a unique in that a large portion of the base is a highly managed wildlife management area where prescribed burns are frequently carried out to restore habitat. Aside from military maneuvers, the base is undisturbed and many habitat types are unaltered by urbanization and agricultural changes that may negatively impact small mammal populations.

While competition between mesopredators and ABBs for carrion may be present at FCJMTC, the mostly undisturbed terrain may still be home to a vast number of small vertebrates that provide ABBs the carcasses required for successful reproduction. Competition for carcasses between ABBs and mesopredators may be a contributing factor in the ABB decline and I recommend further research to understand associations between these species. Based on my findings, ABB management tactics could be improved by reducing optimal Virginia opossum and northern raccoon habitats by reducing woodland habitats and focusing on open habitats such as grassland. Furthermore, increasing interior habitat and avoiding small, fragmented areas or edges for reestablishing ABB populations may help enrich habitat for ABB and decrease optimal habitat for mesopredator competitors.

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CHAPTER 2 FIGURES AND TABLES

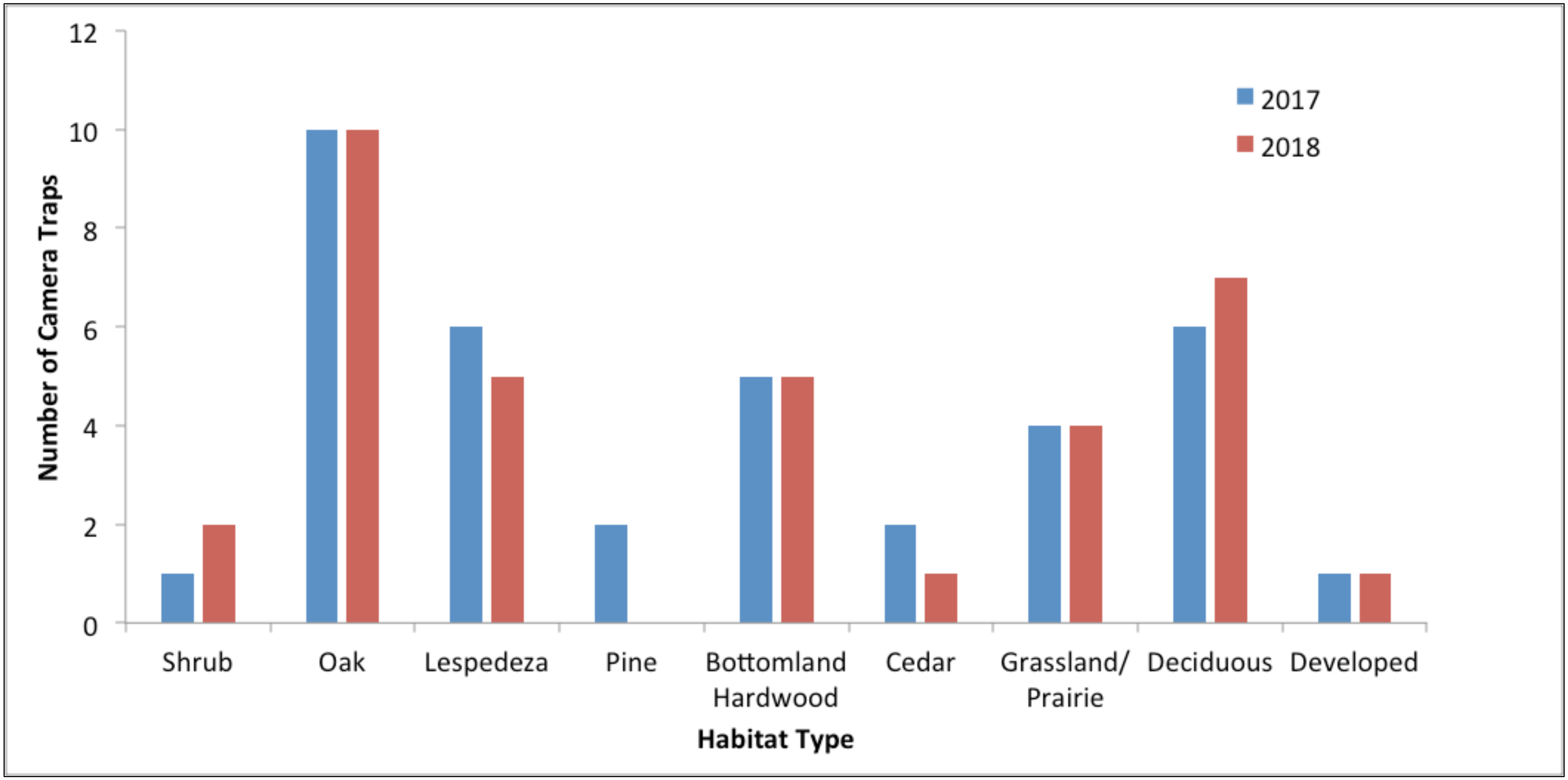

Figure 2.1. Total number of camera traps placed on ABB traps in each habitat type in the 2017 and 2018 seasons.

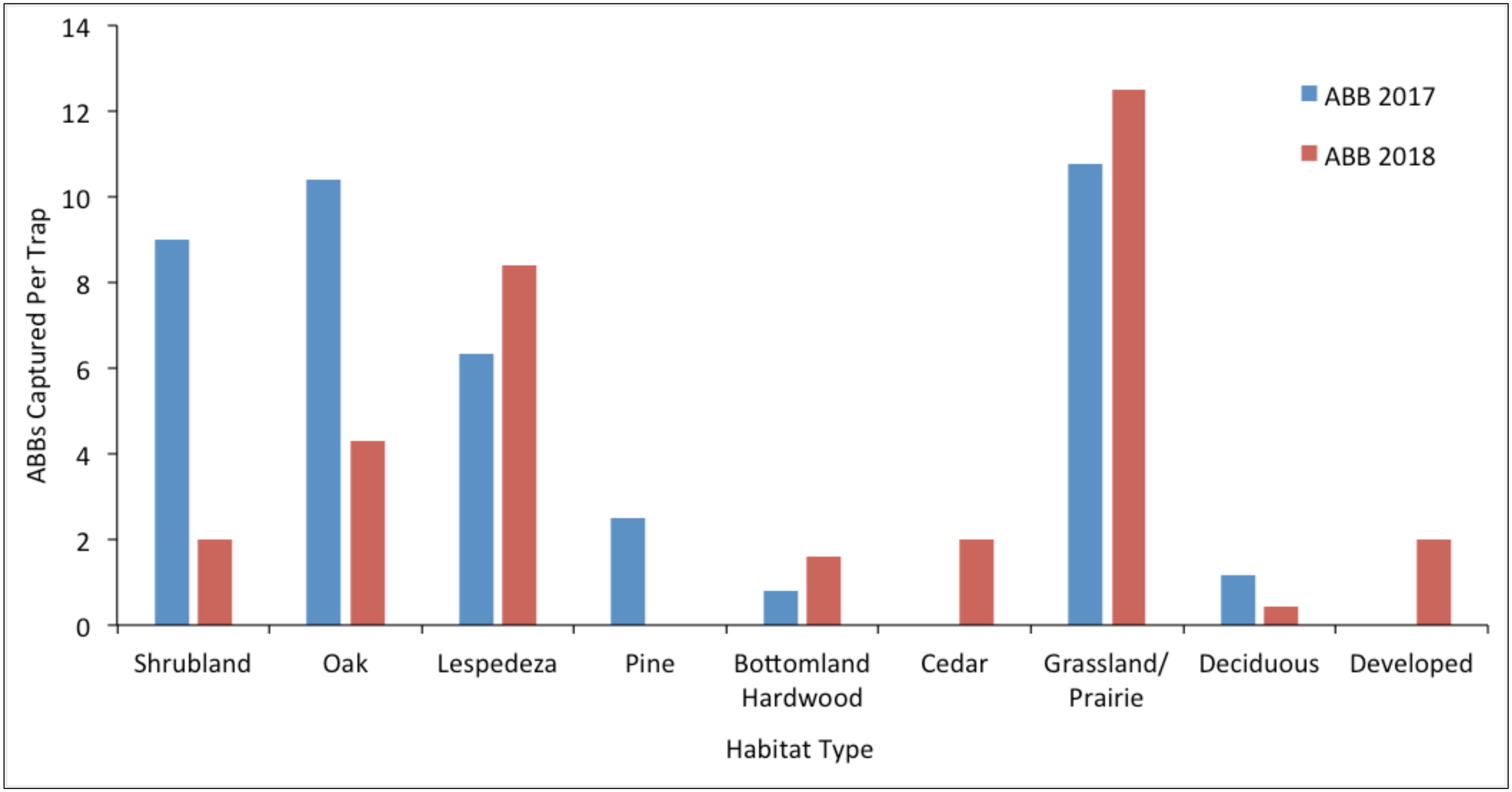

Figure 2.2. Total number of ABBs captured per trap by habitat type over the two seasons.

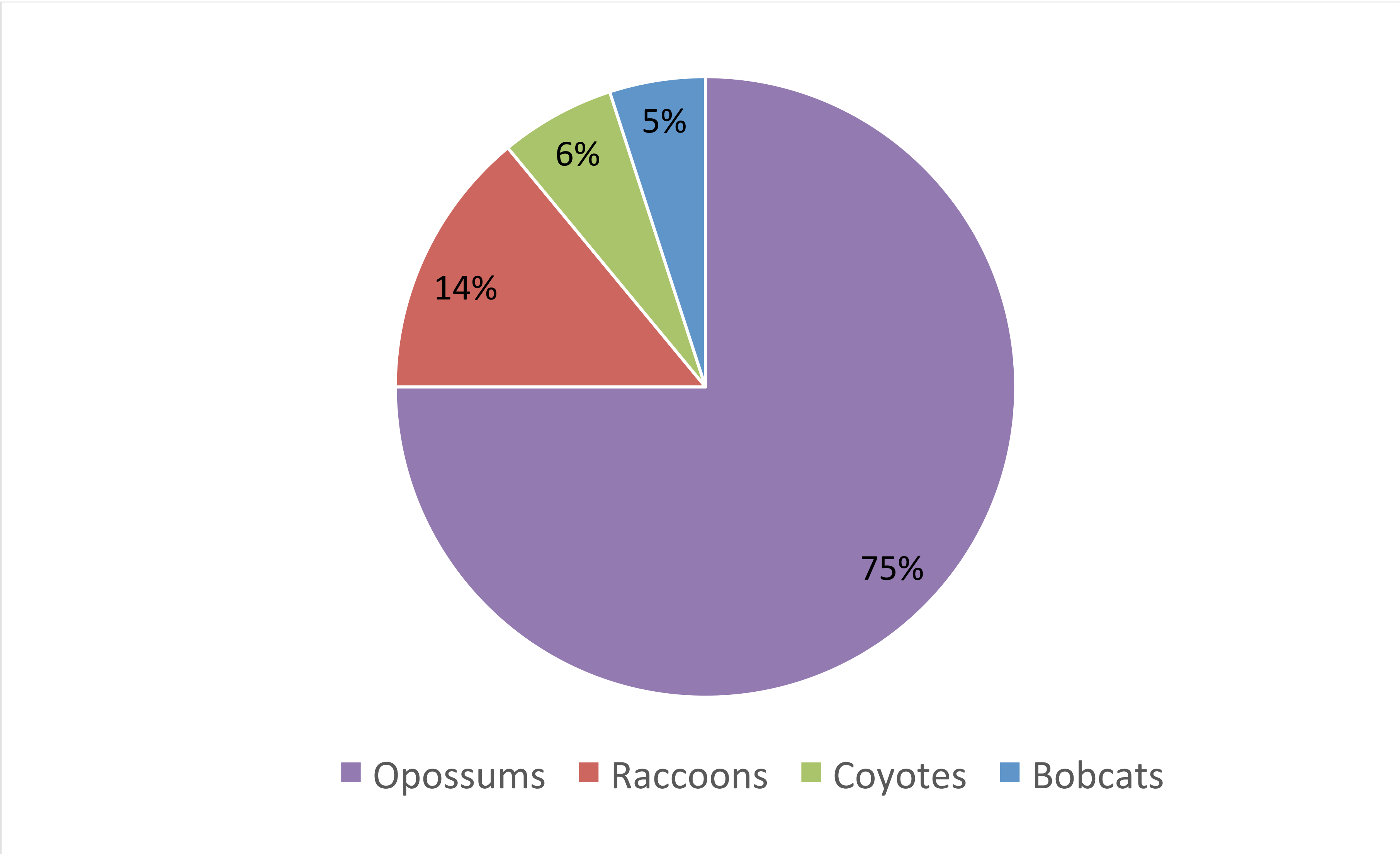

Figure 2.3. Proportion of each species of mesopredator captured during the 2017 and 2018 seasons.

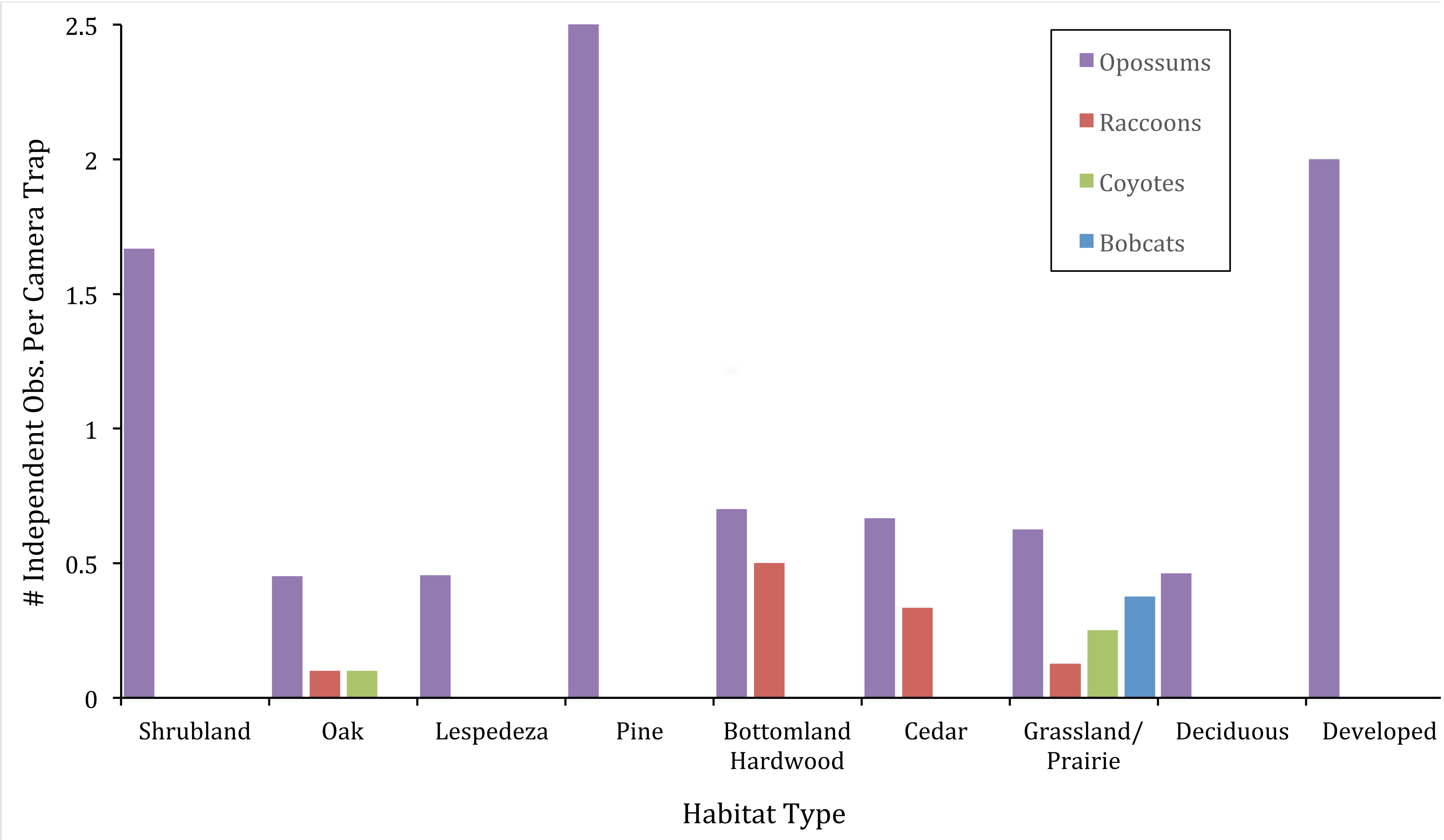

Figure 2.4. Independent mesopredator species captures per camera trap by habitat type over the two seasons.

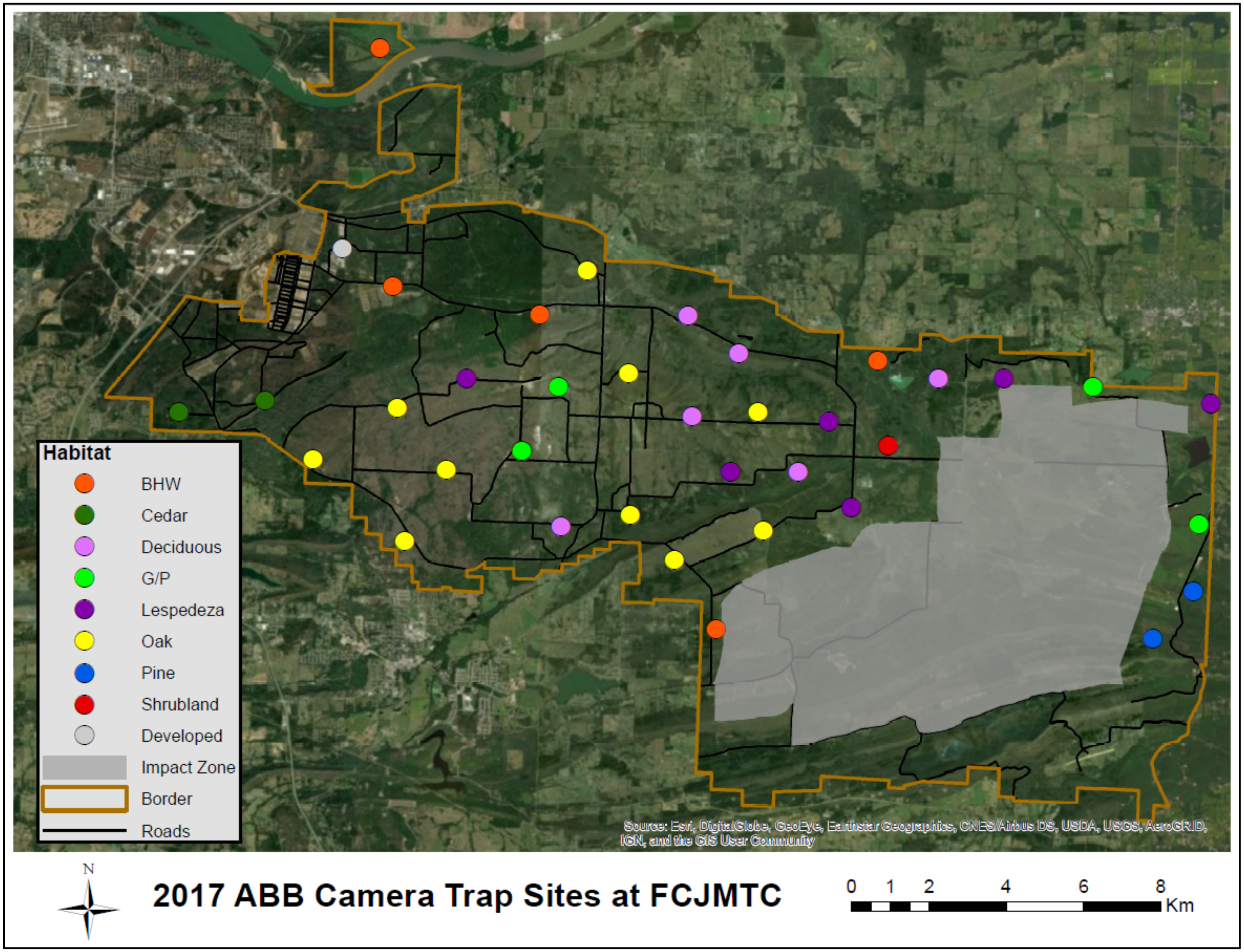

Figure 2.5. Camera trap sites by habitat type for the 2017 season.

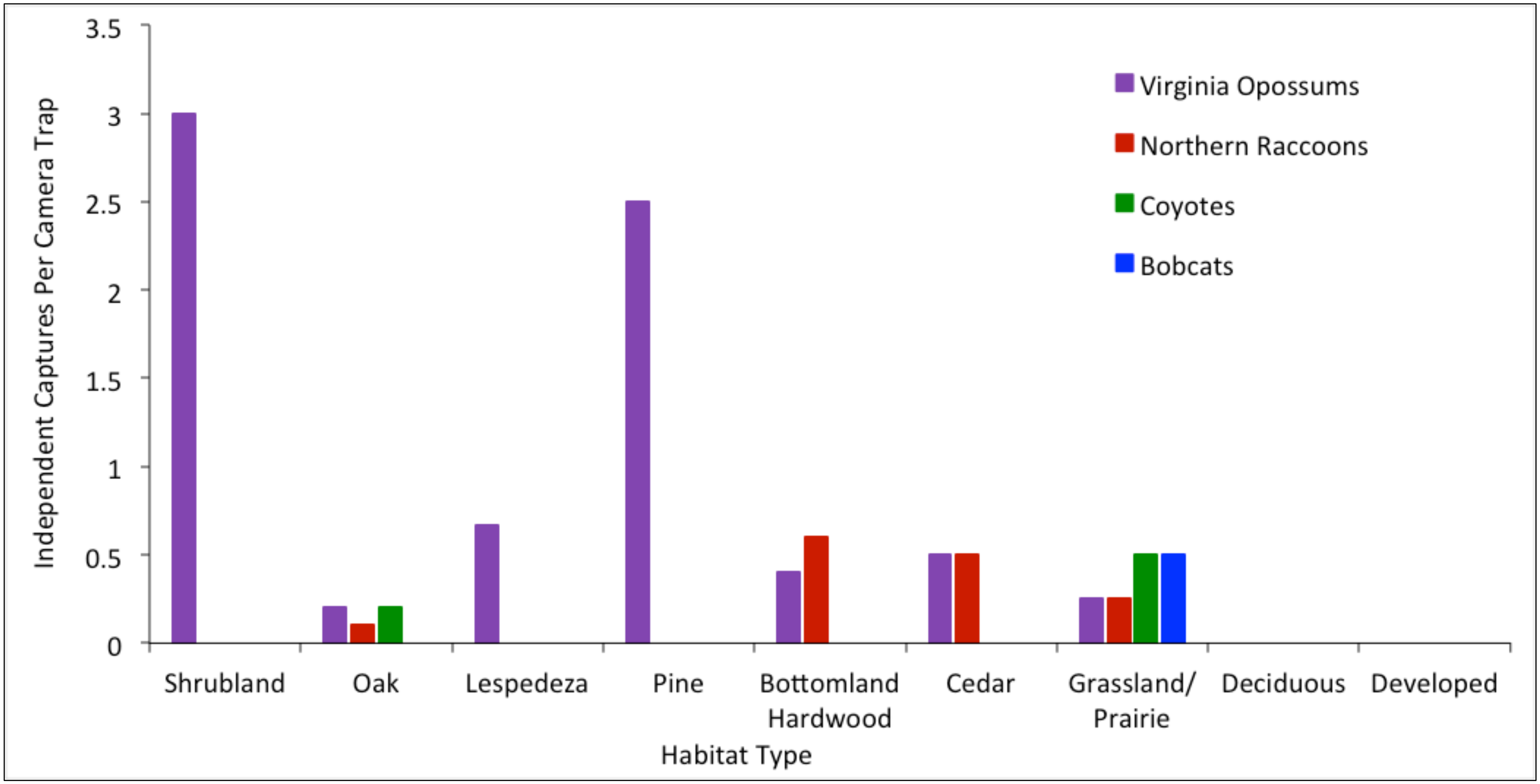

Figure 2.6. Independent mesopredator captures by habitat type for the 2017 season.

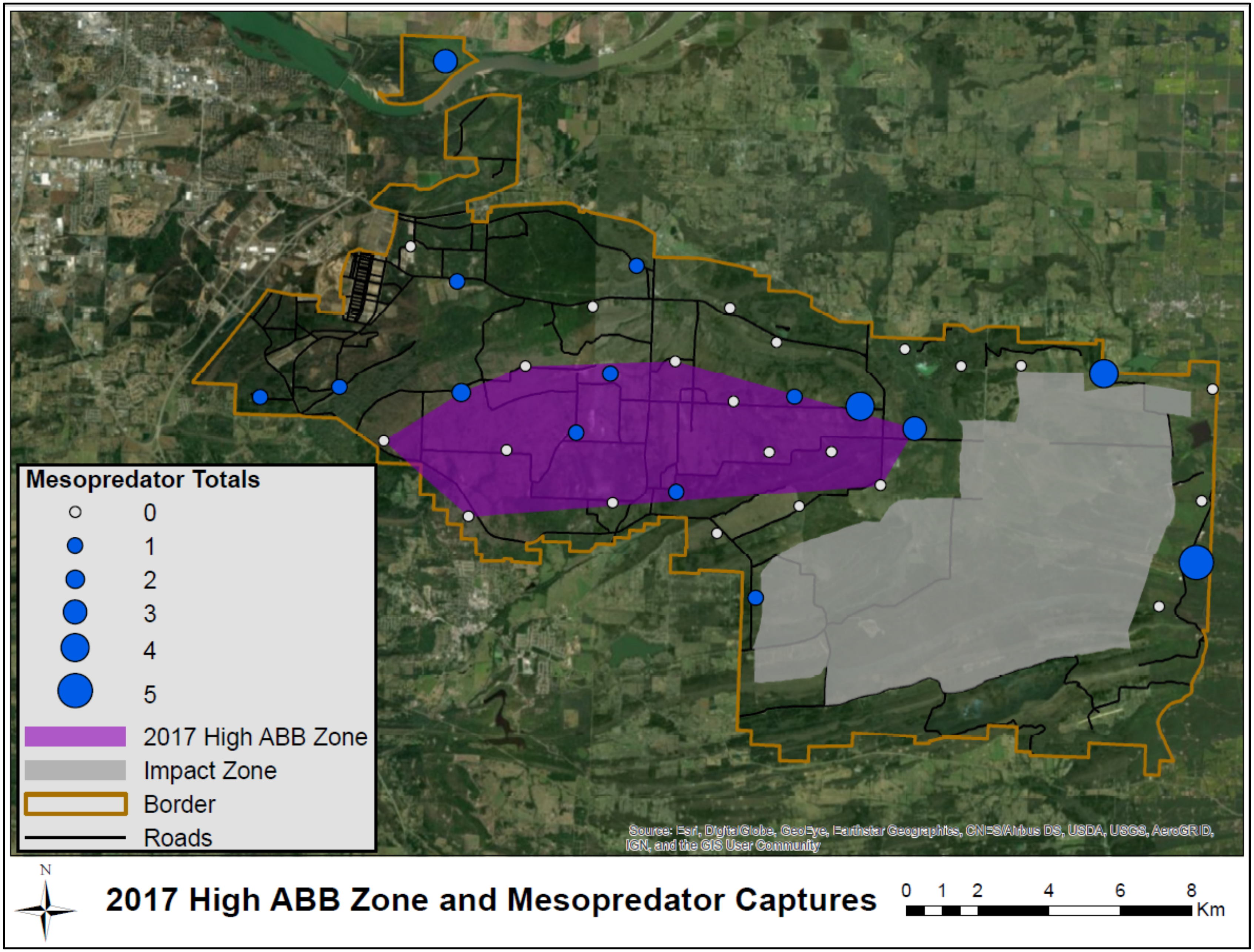

Figure 2.7. Mesopredator captures by site for the 2017 season overlaid with 2017 high ABB zone convex polygon.

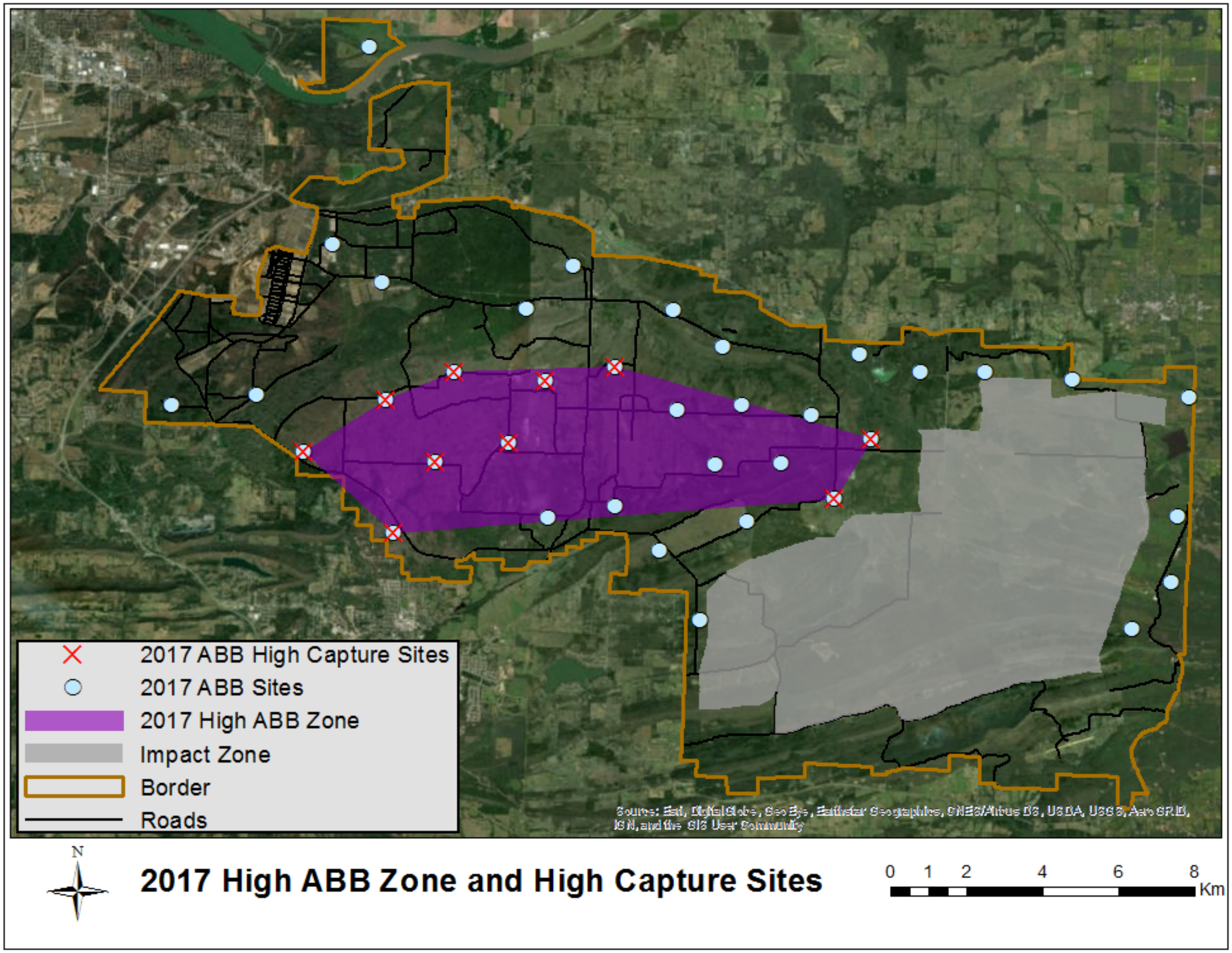

Figure 2.8. ABB trap sites where mesopredators were monitored in 2017 and high ABB capture sites where more than 5 ABB were captured over the 3 night trapping period overlaid with 2017 high ABB capture zone convex polygon.

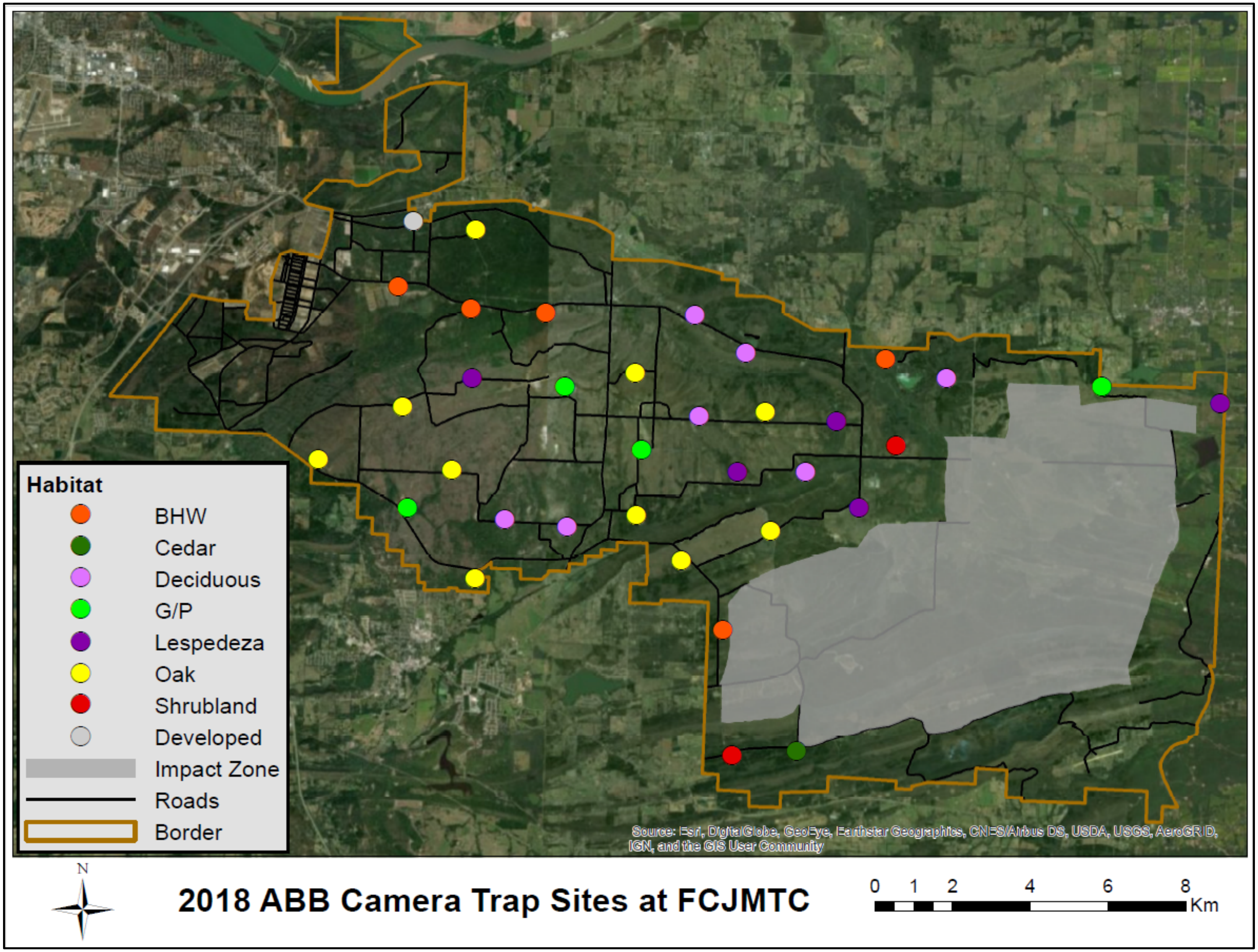

Figure 2.9. Camera trap sites by habitat type for the 2018 season.

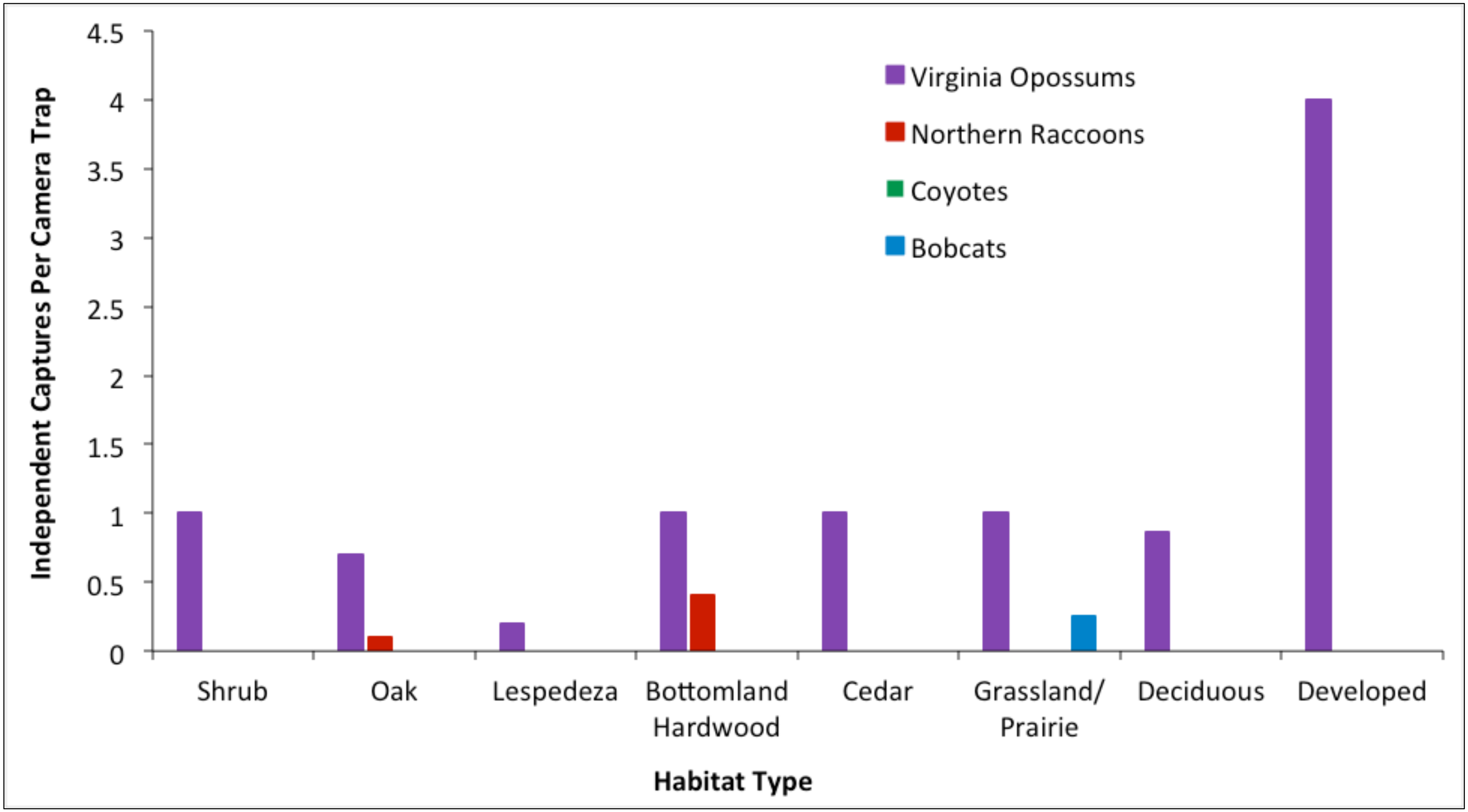

Figure 2.10. Independent mesopredator captures by habitat type for the 2018 season. No cameras were placed in the pine habitat this season.

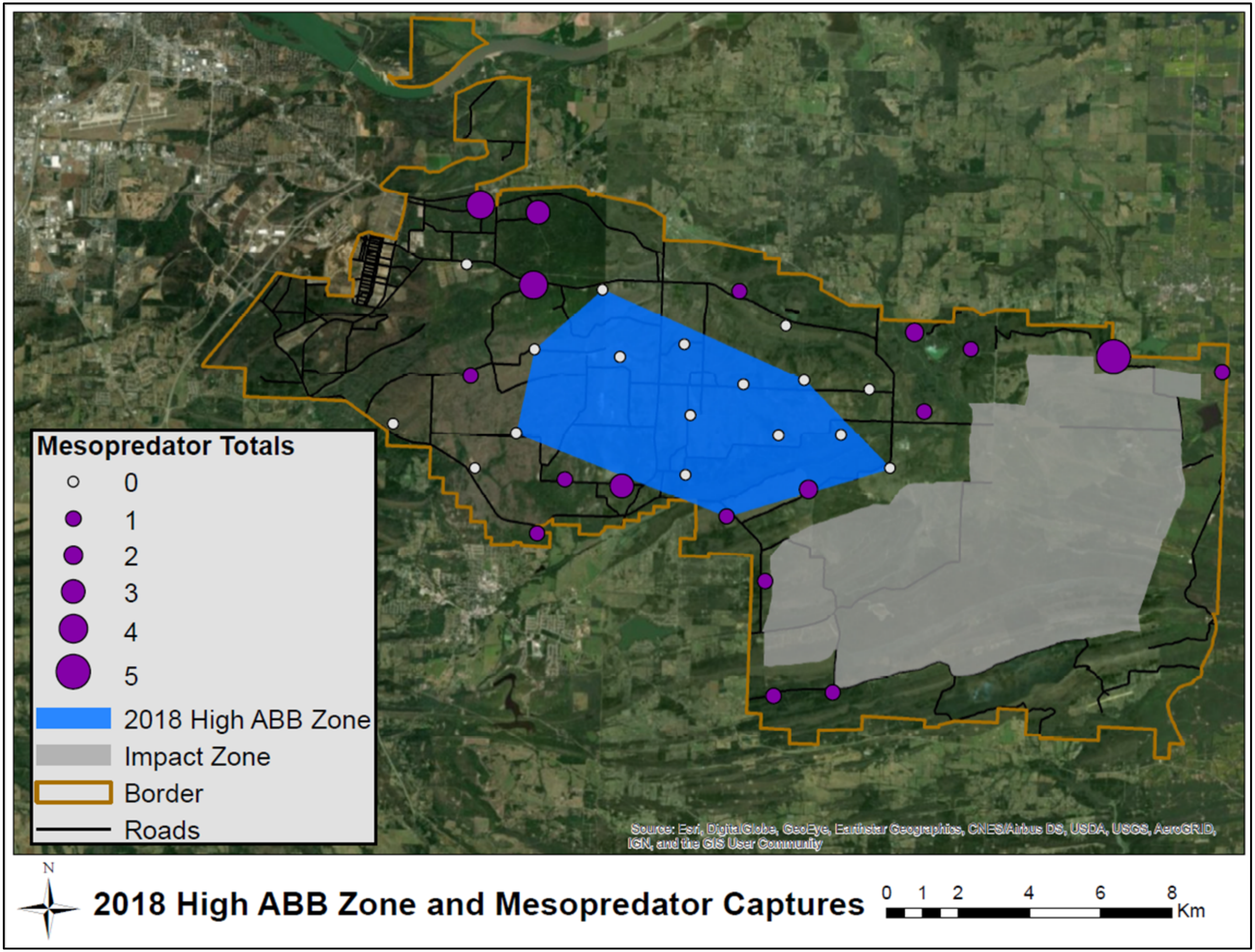

Figure 2.11. Mesopredator captures by site for the 2018 season overlaid with 2018 high ABB zone convex polygon.

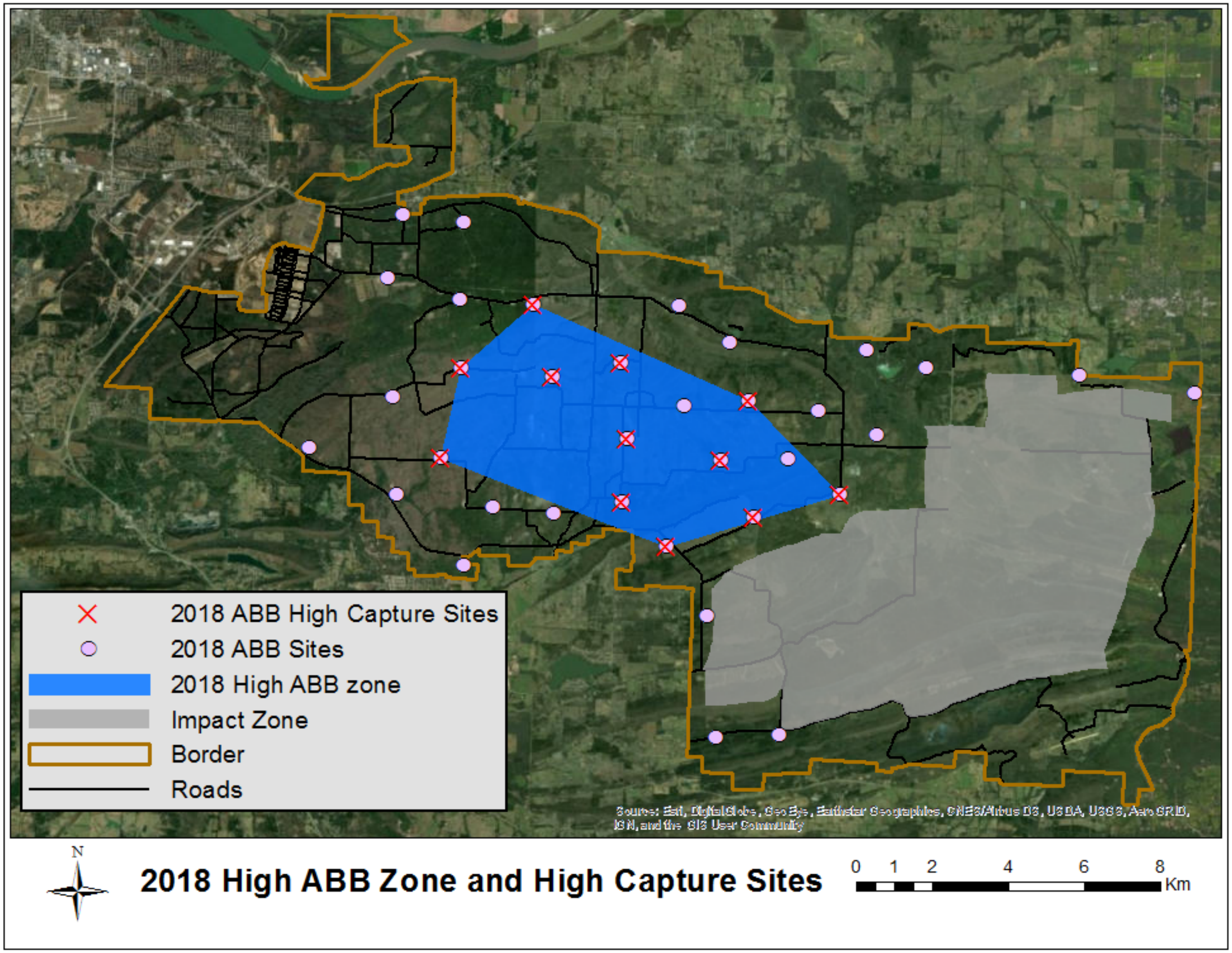

Figure 2.12. ABB trap sites where mesopredators were monitored in 2018 and high ABB capture sites where more than 4 ABB were captured over the 3 night trapping period overlaid with 2018 high ABB capture zone convex polygon.

Table 2.1. Total photos and ABBs captured over the two seasons at FCJMTC.

	2017	**2018**	**Total**
Total Photos	17,530	31,468	48,998
False-triggers	13,062	28,010	41,072
Total Cameras	37	35	72
Total Trap Nights	111	105	216
ABBs Captures	210	154	364

Table 2.2. Independent sightings of each species by season captured at FCJMTC.

Independent Sightings	**2017**	**2018**	**Total**
Virginia opossums	18	30	48
Northern raccoons	6	3	9
Coyotes	4	0	4
Bobcats	2	1	3
Pigs	1	2	3
Deer	2	0	2
Armadillos	1	1	2
Wild turkey	1	0	1
Vulture species	20	19	39
Other	1	5	6
Total	56	61	117