HABITAT-SPECIFIC VARIATION IN MAMMAL COMMUNITIES USING CAMERA TRAPS IN WESTERN TEXAS

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Abstract

Multiple-species analyses are useful to wildlife managers concerned with community-level interactions, habitat use, and landscape connectivity. In western Texas, the community-level habitat use of mammals is not known. I combined ordination techniques with a community-level camera trap study across western Texas to examine variation in mammalian habitat use along environmental gradients within and across three study sites. I initiated a camera trap study from September 2014 to October 2015 across an east-west gradient in western Texas to address which environmental variables most influenced habitat use in a small to large mammal community. I stratified camera traps (n=16) across 4 coarse habitat types (upland, lowland, midslope, drainage) in each of three study sites: Buck Hollow Ranch, Independence Creek Preserve, and Black Gap Wildlife Management Area. Cameras captured 1,017,864 images across all 3 sites, and were combined with camera-specific environmental variables (n= 63) and fragmentation statistics in a canonical correspondence analysis (CCA). Habitat use by 40 mammal species across the 3 sites in western Texas exhibited weak associations with the selected environmental variables. The CCA showed 40 out of 63 possible environmental variables were significant for explaining variation in mammal community habitat use, though patterns of habitat use were weak for all 40 individual species. A cluster of species were positively, albeit weakly, associated with upland habitat type, including. black-tailed jackrabbit, burro, kit fox, kangaroo rat, and American badger. I found no evidence of

habitat partitioning amongst any species detected in this study; it is possible that mammal communities in western Texas are structured temporally and not spatially. Because spatial organization of wildlife communities is associated with habitat selection and use and prey availability, the results of this study may suggest that the habitat in these 3 study areas is high quality. I found that all 40 of the species surveyed use diverse habitat, which provides baseline information from which to generate new questions for Texas wildlife management. Future examinations should consider other landscape variables in order to more effectively understand how communities perceive and use habitat types, and, given the size of these datasets, analyses may be more beneficial when restricted to ecologically similar groups. My study demonstrates that remote cameras can be used to survey multiple species simultaneously using a stratified study design.

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HABITAT-SPECIFIC VARIATION OF MAMMAL COMMUNITIES USING CAMERA TRAPS IN WESTERN TEXAS

INTRODUCTION

Determining the habitat associations of mammal species is important to the understanding of basic ecology of wildlife and how habitat variation influences community structure. The habitat use of individual species as well as species assemblages can also provide information for wildlife and habitat management. Habitat use is defined as how an animal uses the physical and biological resources in a habitat, where the environmental components needed for an animal's activity may vary on a seasonal or annual basis (Kraussman 1999). Numerous studies have investigated the habitat use of individual species; such as red wolves (*Canis rufus*, Karlin et al 2016), duikers (*Cephalophus* spp., Bowkett et al 2008), snowy owls (*Bubo scandiacus*, Chang 2017), ocelots (*Leopardus pardalis*, Harveson et al 2004), and alligator snapping turtles (*Macroclemmys temmincki*, Harrel et al 2006). However, few studies have tried to simultaneously investigate an entire medium to large-sized mammal community. For studies examining multiple-species wildlife communities, benefits include increasing the ecological effectiveness of management, elucidating species interactions, and understanding the functional dynamics of ecosystems (Soule et al 2003). However, studies of this scale involve logistical difficulties of live trapping such a suite of organisms.

Fortunately, modern camera trapping offers a means to help gather such data. Camera technology has long become a standard tool for wildlife management and research, particularly because this research technique allows for the noninvasive monitoring and detection of wildlife without the need for time-intensive and invasive field sampling methods such as capture or marking. Camera trapping allows for simultaneous data collection across many locations over a long period of time, and can detect diverse taxa. These photographic detections can be used for a variety of field applications in wildlife management, including obtaining estimates of density and abundance (Kelly and Holub 2008), investigating population dynamics (Karanth 2008), survival and reproductive estimates (O'Connell et al 2011), and examining predatory-prey spatio-temporal interactions (Weckel et al 2006), and significantly advanced the study of elusive carnivore behavior (Troillet et al 2014). These data may also produce photo vouchers of rare or difficult to detect species, which can be beneficial for baseline inventories as well as community-level monitoring. Indeed, camera traps have been used to investigate a plethora of wildlife research objectives, including for multiple species research (Kelly and Holub 2008, O'Connell et al 2010) and niche partitioning and species coexistence in multiple-species assemblages (Di Bitetti et al 2008).

However, one of the difficulties of analytically examining community level structure is that traditional statistical methods, such as analysis of variance (ANOVA), have assumptions that are difficult to meet for all species sampled in a particular community. As a result, studies that often sample many species only analyze data for a subset of the species detected (usually the most abundant) and this tends to create a situation where interpretations are derived from a series of single species effects instead of conclusions about the broader community (Tobler et al 2008). Although community metrics, such as species diversity, allow interpretation about how a broader community is influenced by something like habitat or treatment, these metrics do not allow us to look at species patterns within the community (Magurran 1988). This is because ecological processes are often intercorrelated; fortunately, multivariate analyses can help managers interpret the joint relationships of variables in data. Multivariate ordination was developed for exploring variation in plant communities across environmental gradients (ter Braak 1986). Thus, ordination techniques relax some of the assumptions placed on more parametric statistics like ANOVA, and allow for exploration of patterns across all species involved simultaneously regardless of rarity (Palmer 1993).

Community-level camera trap studies can be combined with ordination techniques to help describe variation in habitat use along environmental gradients within and across study sites. Direct gradient analyses, where species are related to environmental factors, can employ camera trap data to ascertain the relative influence of variables and gradients on variation in samples. One such technique useful in detecting spatial patterns is Canonical Correspondence Analysis (CCA). This analysis is ideal for examining relationships between species and their environment with the goal of identifying gradients in environmental variables (ter Braak and Verdonschot 1995). This method builds on ordination by adding the methodology of regression to correspondence analysis, and can help ecologists and wildlife managers understand how multiple species respond to environmental variables (ter Braak and Verdonschot 1995). Researchers can use CCA to measure species and environmental data across axes (gradients). If measured environmental variables correlate strongly to the first few ordination axes, the environmental variables are considered predictors for the sample variation seen in the species composition (ter Braak 1986). For camera trap studies using CCA, the photographs serve as the species matrix. These tests can be used in combination with Geographic Information Systems (GIS), which effectively represent spatial features of landscapes in a myriad of ways. Thus, camera trap studies should be ideal to use GIS for correlating land use maps, topographical maps, or climatic effects with measures of species occurrence or habitat use.

In Texas, habitat use by a mammal community has not been well explored, and previous research on wildlife habitat use in the state has not focused on large-scale variation (Grant et al 1985, Jackson et al 2005). Previous research on habitat use by one or a few mammalian species across Texas has been used to justify habitat restoration for ocelots (*Leopardalis pardali*s, Harveson et al 2004), identify vegetation compositions that promote coexistence between sympatric mule and white-tailed deer species (*Odocoileus hemionus* and *Odocoileus virginianus*, Brunjes et al 2006), advocate for the conservation of native short-grass prairie for habitat specialists such as the swift fox (*Vulpes velox*, Kamler et al 2006), and identify conditions that provide competitive advantage to peccaries (*Tayassu tajacu*) over invasive feral hogs (*Sus scrofa*, Ilse and

Hellgren 1995). Because habitat use is influenced by an animals' resource needs, descriptions of larger suites of wildlife mammalian species across environmental gradients can be informative for individual species and community-level interactions. Both are useful to varying levels of wildlife management. However, the majority of Texas is privately owned (97%), and wildlife are managed very differently throughout the state. Western Texas comprises a variety of ecoregions and concordant macrohabitat breaks, with estimated mammalian species diversity being greater in western Texas than in eastern Texas (Schmidly and Bradley 2016). Understanding the influences of habitat on mammalian communities is integral to local and regional wildlife management, as one species may respond to environmental variables differently in different parts of the state, or be influenced by the presence of another species. Understanding these ecological relationships is particularly for those species that provide economic benefit through hunting and trapping. A large-scale camera trap study investigating variation in mammal community habitat use, then, should be beneficial to both the ecology of individual wildlife species in the state as well as understanding what environmental components influence broad community structure, including fur-bearing mammals and non-game animals. Examining multiple-species will be useful to understanding how environmental variables impact the spatio-temporal dynamics of community-level habitat use. My objective was to initiate a camera trap study along a gradient in western Texas to address which environmental variables most influence habitat use by a diverse mammal community.

METHODS

I examined mammalian habitat use across 3 study sites in western Texas: Buckhollow Ranch, Independence Creek Preserve, and Black Gap Wildlife Management Area (WMA). These 3 properties create an east-west gradient of approximately 334 km (Figure 1). Buckhollow Ranch, the easternmost of the 3 study sites, is located in Real County and Uvalde County on the Edwards Plateau. Buckhollow Ranch is a private property that is primarily managed for hunting. Elevation ranges on the property from 509 meters to 680 meters above sea level. This area is the most heavily vegetated of the three study sites with oak (*Quercus sp.*), juniper (*Juniperus sp.*), Texas mountain laurel (*Sophora secundiflora*) being the dominant woody species. The spring fed Dry Frio River runs through the property and is fed by several springs that well up on the area. Lowland areas are largely open grasslands with interspersed oak mottes. Along the river, American sycamore (*Platanus occidentalis*) dominates. Heavily vegetated slopes lead to small uplands. Juniper, Texas mountain laurel, and oak are found on the slopes and hill tops. Independence Creek Preserve (ICP) is located in Terrell County, Texas, approximately 75 km north of the Texas-Mexico border. This 7,988 hectare property, owned and managed by The Nature Conservancy, was created by the purchases of the Oasis and Canon Ranches in 2000 and 2001 respectively. Independence Creek, the body of water for which the preserve is named, bisects the property as it flows into the Pecos River. Elevation on the site ranges from 579 meters to 762 meters above sea level. On either side of the creek, the area is composed of high, flat-topped plateaus with carved limestone canyons that feed into lowland washes before leading to the creek. The tops of the plateaus are vast, flat, open grasslands with juniper interspersed across the landscape. Wooded canyons lead down from the tops of the plateaus and are dominated by juniper. Lowland areas are a mix of mesquite and juniper grasslands, creosote flats, and live oak mottes. The oak mottes provide the most canopy cover found on the site and only occur in patches proximal to the creek. This area lies on the transition zone between the Edwards Plateau and Trans Pecos ecological regions of Texas (Gould 1978).

Black Gap WMA is located in Brewster County, Texas. The largest of the three study sites at 103,000 acres, Black Gap WMA is bordered to the west by Big Bend National Park and to the south by the Rio Grande. Elevation on the site ranges from 1600 feet above sea level at the banks of the Rio Grande to over 4600 feet above sea level at the highest peaks. This area is firmly within the Trans Pecos ecoregion of Texas as described by Gould (1978). The dominant vegetation is a mix of creosote bush (*Larrea tridentata*), prickly pear cactus (*Opuntia spp.*), and honey mesquite (*Prosopis glanudlosa*). Expansive creosote monocultures make up most of the lowland areas within the study site. Large upland mesas rise sharply over the surrounding landscape with the more gently-sloping, rocky, igneous hills provide additional topographic relief. Arroyos, or dry creek beds, dissect the area and wind their way toward the Rio Grande.

I stratified 16 Bushnell Trophy cameras (Bushnell Corp., Overland Park, KS, USA) across 4 coarse habitat types on each site for the duration of this study (Figures 2,3,4). These habitat types were categorized as lowland, midslope, upland, and drainage habitats. These coarse habitat delineations were made to ensure that they would be applicable to all 3 study sites. Several generations and models of Bushnell Trophy Cam were used over the duration of the study because of changing availability. Thus, I used Bushnell Trophy Cam Standard Edition, Bushnell Trophy Cam HD, Bushnell Trophy Cam HD Max Black LED, and Bushnell Trophy Cam HD Essential E2 cameras, but I was careful to deploy the different types throughout the 3 study sites and different habitats. However, >80% of cameras deployed at any given time were either Trophy Cam Standard or Trophy Cam HD models.

Cameras were set along game trails or near areas with evidence of animal activity and were spaced a minimum of 1 kilometer apart from each other. One kilometer distance between camera site locations was used to attempt independence between all cameras. Camera traps were always secured in a CamLockBox (CAMLOCKbox, Green Bay WI, USA), a metal enclosure that mounts the camera trap to an object. The enclosure was then secured with a keyed lock or cable lock to prevent theft. Whenever possible, cameras were mounted to trees, but when trees were not present, plywood stands were employed to mount the camera. Plywood stands measured 61cm tall and 30.5 cm wide. Stands were "Z-shaped" with 2-30.5 cm by 30.5 cm square sections which were attached to a 61 cm long vertically aligned section . This allowed the stands to have both a base that allowed them to stand upright and a roof over the camera that shaded it from direct sunlight. Whenever possible, cameras were aimed in a northerly direction to reduce glare (between 330° and 30°). A GPS point was recorded for each camera location using a Garmin eTrex 30 GPS unit (Garmin Ltd., Olathe, KS, USA). Each location was averaged to produce an error rate of <5m for each coordinate.

Cameras were programmed to take three pictures in rapid succession each time they were triggered. This was done to increase the likelihood that at least 1 of the 3 images would allow for confident identification of the species that was photographed. After being triggered, the cameras were programmed to not fire again for at least 10 seconds. All cameras were set at the most sensitive detection setting. The area around the camera detection zone was landscaped to remove branches and herbaceous vegetation that might trigger the motion sensors of the cameras. This landscaping was repeated each time cameras were checked.

I set cameras in September 2014 and monitored them through October 2015. Cameras were checked about every three months at which point the batteries and SD card were replaced. If a camera failed or malfunctioned, it was replaced with the closest model available. Once removed from the field, images were downloaded from the SD cards and saved onto 2 different external hard drives that were stored in 2 separate physical locations. Images were then scored by being viewed and translated into text form in a Microsoft Excel spreadsheet. Each image was represented by a row in the spreadsheet, and all information written onto each image was recorded in that row: filename, date, time, temperature, and barometric pressure. Temperature and barometric pressure were not recorded by every camera, and they were excluded from the spreadsheet when not available. Each mammal species that was encountered was given a column in the spreadsheet. When a mammal species was observed in an image, the number of individuals of that species was recorded under its respective column.

I used CCA (ter Braak 1986) as a direct gradient analysis technique, where species composition is directly related to environmental variables. For this analysis, each camera during each month acted as the experimental unit within the species matrix.

In order to turn thousands of images into a single number for each species during each camera-month for this species matrix, an importance value was created. This value is meant to represent the importance or level of use of a specific site to a species. Calculating such an index of use is relevant, because individuals cannot be reliably identified from camera images. Additionally, importance of a site could come about in 2 different ways. I considered a habitat important regardless of whether a site was used rarely by many individuals or if it was used commonly by single individuals. Thus, focusing on importance value instead of individuals reduces the need to worry about independence of images. Also, because of camera malfunction, not every camera was operating for the same period of time. As a result, camera-days, the number of days that a camera was operational, was incorporated into the importance value. The result is the following equation that was used to calculate an importance value for each species for each camera-month combination:

$$\left[\left(\frac{Number\ of\ Events\ a\ Species\ was\ Detected}{Camera\ Days}\right) \times \left(\begin{matrix}Average\ Number\ of\ Individuals \\ of\ the\ Species\ per\ Event\end{matrix}\right)\right] \times 10$$

Analytically, this resulted in an importance value being calculated for every species for each camera-month. A camera-month is a calendar month in which an individual camera was operating.

To identify camera-specific environmental variables for the CCA environmental matrix, I buffered each camera with a 500 m radius polygon within ArcView 3.3 (Environmental Systems Research Institute, Redlands, California, USA). These buffer polygons were then laid over 2008 Texas Orthoimagery Program Color Infrared (CIR) aerial photography layers (Texas Natural Resource Information System, Austin, Texas, USA) of each study site. Color infrared imagery, also called false-color imagery, is specifically helpful for vegetative analysis because it causes rapidly-growing vegetation to show up red. The amount of vegetative cover within the buffer polygons was digitized into 3 distinct classes: high, medium, and low (Figure 5). The high cover class represented 80 – 100% vegetative cover, the medium cover class represented 31 – 79% vegetative cover, and the low cover class represented 0 – 30% vegetative cover. Prior to digitization, a minimal mapping unit of 5 m^2 was designated.

After digitizing habitat polygons, I used Patch Analyst 3.1 (Rempel et. al 2012) to develop fragmentation statistics based on the different vegetative cover classes. The fragmentation statistics that were included in the environmental matrix were class area, number of patches, mean patch size, standard deviation of patch size, total edge, edge density, mean patch edge, mean perimeter-area ratio, Shannon’s diversity index of patch size, and evenness of patch size. When applicable, these statistics were calculated for both the entire buffer polygon as well as each vegetative cover class, and were used as variables in the environmental matrix. Additionally, I selected climatic variables and environmental variables that occurred in each of the four coarse habitat types, including variables previously determined to be informative to mammalian habitat use (Beier and

McCullough 1990, Davis, I.A. 2015, Dennison et l 2016, Stevens, S. 2017). To account for seasonal variation, I included the 12 months as variables. In total, I used 63 environmental variables for the CCA (Table 1). All spatial analyses were performed using ArcView 3.3 (Environmental Systems Research Institute, Redlands, California, USA)

These analyses produced 2 files: A species matrix comprised of importance values for each species within each camera-month, and an environmental matrix containing fragmentation statistics, climatic variables, and environmental variables. I processed these matrices for the CCA using CANOCO ver. 4.5 (Program CANCOCO ver. 4.5 February 2002). I used the Monte Carlo forward selection procedure with 1000 iterations within the core program to evaluate the significance of each environmental variable. Data were not transformed for this analysis, and months with less than 15 camera days were excluded from the analysis.

RESULTS

Cameras captured 1,017,864 images across all 3 sites. Independence Creek Preserve had the largest amount of images with 406,364, followed by Black Gap WMA (383,694) and Buckhollow Ranch (227,806). Images containing mammals accounted for 11.15% (113,505) of all images. Clear images, or images that were taken without any distinguishable animal trigger, accounted for 87.46% (890,273) of all images. Only 378 images were designated as unknown. In these images, the animal that triggered the camera was not identifiable to species. Often only a small part of the animal was captured on the edge of the frame because of the animal moving at a rate too great for the trigger speed of the camera trap. Images of other animals accounted for 13,708 of the images. This was largely comprised of images or birds including turkey, turkey vulture, roadrunner, and several species of songbirds. Reptiles were also occasionally captured on the images. In many cases, it was unclear whether this was because of the animal triggering the camera or if the animal simply happened to be in the frame during a random camera event.

Across the entire study, 40 taxa of mammal were detected (Table 1). Because of their size and behavior, the exact species of bats and mice could not be determined from the camera trap photos. As a result, all bats, regardless of species, were grouped as "bat," and all mice were grouped as "mouse."

Buckhollow Ranch was the most species rich site with 30 species observed. Twenty-nine species were observed at both Black Gap WMA and Independence Creek Preserve. At Buckhollow Ranch, 38,820 of the 227,806 images captured contained mammals. This site had the fewest camera trap images of all three sites, but ranked second in terms of number of mammal images. Northern raccoons (*Procyon lotor*) were the most captured species with 6,840 images followed closely by white-tailed deer (*Odocoileus virginianus*) with 6,160 images. Feral hogs (*Sus scrofa*) were the next most observed species with 5,169 images, and it is notable in that the third most observed species is an invasive species. The eastern cottontail (*Sylvilagus floridanus*) was the fourth most recorded species with 3,872 images captured. The non-native aoudad (*Ammotragus lervia*) finished the 5 most observed species with 2,884 images.

Buckhollow Ranch had the largest number of exotic species observed with 6: feral hog, aoudad, axis deer (*Axis axis*), sika deer (*Cervus nippon*), fallow deer (*Dama dama*), and feral sheep (*Ovis aries*). These six non-native species comprised 27.10% of all images taken.

Independence Creek Preserve produced the most camera trap images and most images of mammals of all 3 sites. Of the 406,364 images taken, 51,787 contained mammals. Independence Creek Preserve was heavily dominated by 1 species, white-tailed deer. A total of 22,674 images contained white-tailed deer, accounting for 43.78% of all images of mammals captured at the site. Gray fox (*Urocyon argenteus*) was the second most observed species (5,676 images), and was 1 of only 2 species to occur at all 16 cameras. Rock squirrel (*Otospermophilus variegatus*), javelina (*Pecari tajacu*), and black-tailed jackrabbit (*Lepus californicus*) rounded out the 5 most observed species with 3,946, 3,435, and 3,293 images respectively.

Black Gap WMA had the fewest number of mammal images of all 3 sites with 22,898 of the 383,694 images containing mammals. The cottontail was the most documented species on the site. It occurred in 7,575 images (33.08% of all pictures containing mammals) at 15 of the 16 camera traps. Gray fox ranked second in terms of number of images with 3,358 across 15 of the 16 camera traps. Similar to Independence Creek Preserve, black-tailed jackrabbit, rock squirrel, and javelina were among the 5 most observed mammals with 2,534, 2,439, and 1,920 images respectively. Notable species documented at BGWMA that did not occur at the other sites were the kangaroo rat (*Dipodomys spp.*), burro (*Equus africanus*), Mexican ground squirrel (*Ictidomys mexicanus*), kit fox (*Vulpes macrotis*), and desert bighorn (*Ovies canadensis*).

The total inertia for the CCA analysis was 7.98. The ratio of the sum of constrained eigenvalues to the sum of unconstrained eigenvalues suggested that the environmental variables in the model justified 3.49% of the variance in the data. Axis 1 (Eigenvalue 0.589) and Axis 2 (Eigenvalue 0.552) accounted for 32.7% of the explainable variation (Figure 6 and Figure 7). Because of the low percentage of explainable variation, axes beyond Axis 2 had little explanatory power.

The CCA detected that 40 out of 63 possible environmental variables in the environmental matrix were significant for explaining variation in mammal community habitat use (Table 2). Patterns in habitat use were weakly influenced by the majority of the significant variables. Based on the combination of the relatively short length of the biplot arrows for Axis 1 and Axis 2, and the cluster swarm for all 40 mammal species, trends between any individual species and environmental variables were weak (see Figure 8 for an inset of selected environmental variable positions).

In terms of community patterns, a cluster of species were positively, but weakly, associated with upland habitat type. Some of these species were black-tailed jackrabbit, burro, kit fox, and kangaroo rat. Excluding the American badger, which was weakly (but not significantly) associated with upland habitat, no mesocarnivore species were associated with any specific environmental variable. Antelope squirrels, sheep, black bears, and rock squirrels fell away from the biplot arrows of all variables. Habitat fragmentation statistics variables, percent vegetative cover, elevation, rise, and the months October and November were a few of the significant variables in the CCA, but these did not influence the variation in mammal community habitat use.

DISCUSSION

Habitat use by the mammal community across the 3 sites in western Texas exhibited weak associations with the 63 selected environmental variables. Similarly, Grant et al (1985) found a large amount of unexplained variation when testing for correlations between climatic variables and population densities in small mammal communities in central Texas. For my study, I expected to see more habitat associations for individual species, as well as patterns of habitat use between groups of species. For example, Dennison et al (2016) used camera traps in the Davis Mountains of Texas for a similar community-level habitat use assessment and found that coyotes and feral hogs avoided higher elevation habitat, whereas javelina selected for high elevation. When considering the biplot arrows of my CCA, feral hogs are opposite the arrows for elevation and rise, suggesting a negative association. As the percentage of explained variation is so weak, however, I cannot consider this a true association. It is worth noting, however, that despite the low amount of explainable variation, both the presence of feral hogs and coyotes were not located near the biplot arrows for elevation and rise on the CCA. Javelinas were also not associated with this variable in the CCA, which is unlike what Dennison et al (2016) found.

I also expected to see a stronger correlation between fragmentation statistics, such as mean patch size, mean patch edge, and total edge, and the presence of mesocarnivore species. In a literature review focusing on the relationships between landscape heterogeneity and animal diversity, Tews et al (2004) concluded overall positive associations between structural habitat variation and increased species richness. Bobcats have been positively associated with brushy areas (Rolley and Warde 1985), dense understories and prey availability (Litvaitus et al 1986), and increased landscape heterogeneity in Texas (Davis 2015), but I was unable to detect any patterns in bobcat habitat use. In my study, black bear presence had no preference for any habitat type, which is not surprising given their highly mobile and generalist behavior. However, studies on food habitat of bears in Big Bend National Park and Black Gap Wildlife Management Area, one of my study sites, showed that bears use oak-dominated habitat more than expected, likely because of the importance of fall mast production in this region (Hellgren 1993, Onorato et al 2003). Preference for habitat type in coyotes in southwestern Oklahoma was also linked to food availability (Litvaitus 1980), yet no patterns emerged in the CCA for coyotes in western Texas. For all species, including other carnivores and mammals, this could be a function of generalist behavior in highly mobile species, or the result of study design error. This study focused on coarse habitat types, habitat heterogeneity via fragmentation statistics, and climatic variables. It is possible that the correlation between relationship between mammal communities and habitat use might be better examined through analyses of spatial complexity, vegetation complexity, or vegetation composition. Additionally, it may be unfair to consider an "upland" at Buckhollow Ranch to be the same category as an "upland" at Black Gap

WMA. Thus, the artificiality of my categories may be obscuring patterns. It is also possible that my gradients were too short to be adequately patterned with a CCA. Thus, expanding the gradients either spatially or temporally might clarify patterns of habitat use better.

I also did not see evidence of habitat partitioning between sympatric species, such as between mule deer and white-tailed deer. Brunjes et al (2006) found that mule deer and white-tailed deer in western Texas used different vegetation types and elevation within the same study area, but that despite this partitioning, both species overlapped physically. While I detected very weak correlations between the mammal community and habitat use, it is possible that syntopy is occurring through temporal avoidance rather than spatial avoidance. I did not examine temporal variations in this study, however, Gompper et al (2016) found that carnivore community structure was influenced by differential habitat use more than spatial partitioning. If spatial organization is associated with habitat selection and use and prey availability, and the spatial arrangement of resources can influence where individuals occur (Janečka et al. 2006, Azevedo and Murray 2007), the results of this study may suggest that the habitat in my 3 study areas is high quality. For the mammal communities detected in western Texas, it appears that spatial avoidance, at least at camera locations, is not impacting habitat use. Whether or not the relative abundance for some species was impacted by another was beyond the scope of this study, but would be useful to address for wildlife managers going forward.

The weak associations between coarse habitat types and mammal species' use of those habitats could be because of selecting unimportant landscape variables for the ordination analysis. While it appears that many of the 40 mammal species regularly use many of the areas surveyed by camera traps over the course of this study, any correlations between habitat use and landscape variables may not have been detected because ecologically important variables were not tested. For example, other studies have identified fragmentation statistics, such as edge habitat, to be important to the habitat use of several species (i.e., Tigas et al 2002, Sacks et al 2004), yet few of these studies have focused on such a large suite of species. Vegetation type is also known to influence mammal community composition (Williams et al 2002), and these results suggest that future examinations of community-level habitat use should consider the impact of vegetation. The lack of association with mammal presence and habitat use may have been influenced by examining too many species across too few landscape and environmental variables. The majority of species detected in this study are habitat generalists, however, and as such likely use a variety of habitat types within the landscape matrix, which may also explain the low explanatory power of the CCA.

Despite the weak associations produced by the CCA, this study is meaningful for wildlife managers in Texas because it expands upon the usefulness of camera trap studies for wildlife. There is need for camera trap studies to examine multiple species (Kelly and Holub 2008), yet there may be a threshold of usefulness for certain statistical analyses with multiple-species camera data. Ordination analyses, including CCA, are efficient for detecting relationships between environmental and species matrices, but it is possible that the species used were too opportunistic to pattern by habitat variables or my gradients were too short. To gain more information on mammal habitat use, managers may want to incorporate more habitat types, including vegetation data and climatic data, into their analysis (Kelly and Holub 2008), with the number of species considered for a community-level analysis not outnumbering the number of environmental variables tested. Accounting for camera trap bias is also important; this study likely did not suffer from camera bias because many generations and models of cameras being used and the large number of species detected, but managers may want to consider camera bias when interpreting results. Indeed, multiple-species analyses are useful to wildlife managers concerned with community-level interactions, habitat use, and landscape connectivity.

I found that all 40 of the species surveyed use diverse habitat, which provides baseline information from which to generate new questions, such as estimating species abundance, diversity, and evenness. Future examinations of mammalian habitat use in western Texas should consider other landscape variables, such as vegetation composition, average temperature and rainfall, and distance to water as well as barriers to movement in order to more effectively understand how communities perceive and use habitat types. My study demonstrates that remote cameras can be used to survey multiple species simultaneously using a stratified study design. However, when analyzing multiple species, analyses may be more effective if the species considered are restricted to combinations of ecologically similar groups (Brodie et al 2014). For heterogeneous landscapes, camera trapping may also be more effective when combined with other monitoring methods, as certain taxa may be overlooked or lead to erroneous conclusions (Matthew et al 2014). When using camera trap data for large-scale habitat use analysis, managers should target multiple species in order to maximize the detection and monitoring of wildlife, but they should consider the importance of specific landscape variables in addition to coarse habitat type designations.

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Table 1. Number of camera events for each taxa of mammal detected at 3 study sites in Western Texas, 2014-2015.

	Buckhollow Ranch	**Independence Creek Preserve**	**Black Gap Wildlife Management Area**	**Total**
White-tailed Deer (*Odocoileus virginianus*)	2155	7734	0	9889
Cottontail (*Sylvilagus* spp.)	1415	178	2683	4276
Gray Fox (*Urocyon cinereoargenteus*)	532	2004	1178	3714
Raccoon (*Procyon lotor*)	2509	897	31	3437
Feral Hog (*Sus scrofa*)	1819	612	0	2431
Rock Squirrel (*Otospermophilus variegatus*)	176	1366	886	2428
Black-tailed Jackrabbit (*Lepus californicus*)	0	1178	927	2105
Collared Peccary (*Pecari tajacu*)	126	1168	654	1948
Eastern Fox Squirrel (*Sciurus niger*)	721	452	3	1176
Woodrat (*Neotoma* spp.)	1041	2	90	1133
Aoudad (*Ammotragus lerrvia*)	1006	6	44	1056
Mule Deer (*Odocoileus hemionus*)	0	409	384	793
Ringtail (*Bassariscus astutus*)	263	281	234	778

Table 1 con't. Number of camera events for each taxa of mammal detected at 3 study sites in Western Texas, 2014-2015.

	Buckhollow Ranch	**Independence Creek Preserve**	**Black Gap Wildlife Management Area**	**Total**
Axis Deer (*Axis axis*)	665	0	0	665
Mouse (Family Cricetidae/ Heteromyidae)	178	181	182	541
American Hog-nosed Skunk (*Conepatus leuconotus*)	22	370	107	499
Armadillo (*Dasypus novemcinctus*)	390	95	0	485
Coyote (*Canis latrans*)	316	0	125	441
Texas Antelope Squirrel (*Ammospermophilus interpres*)	0	159	146	305
Bobcat (*Lynx rufus*)	117	31	103	251
Striped Skunk (*Mephitis mephitis*)	1	235	13	249
Spotted Skunk (*Spilogale* spp.)	78	16	86	180
Sika Deer (*Cervus nippon*)	177	0	0	177
North American Porcupine (*Erethizon dorsatum*)	41	107	1	149
Elk (*Cervus elaphus*)	124	13	0	137
Virginia Opossum (*Didelphis virginiana*)	28	88	0	116

Table 1 con't. Number of camera events for each taxa of mammal detected at 3 study sites in Western Texas, 2014-2015.

	Buckhollow Ranch	**Independence Creek Preserve**	**Black Gap Wildlife Management Area**	**Total**
Human (*Homo sapiens*)	5	82	21	108
Hooded Skunk (*Mephitis macroura*)	1	80	8	89
Mountain Lion (*Puma concolor*)	1	60	19	80
American Badger (*Taxidea taxus*)	0	8	71	79
Domestic Dog (*Canis familiaris*)	6	30	11	47
Kangaroo Rat (*Dipodomys* spp.)	0	0	40	40
Feral Sheep (*Ovis aries*)	2	31	0	33
Black Bear (*Ursus americanus*)	1	0	30	31
Bat (Order Chiroptera)	1	3	26	30
Feral Donkey (*Equus africanus*)	0	0	29	29
Mexican Ground Squirrel (*Ictidomys mexicanus*)	0	0	21	21
Fallow Deer (*Dama dama*)	11	0	0	11
Kit Fox (*Vulpes macrotis*)	0	0	8	8

Table 1 con't. Number of camera events for each taxa of mammal detected at 3 study sites in Western Texas, 2014-2015.

	Buckhollow Ranch	**Independence Creek Preserve**	**Black Gap Wildlife Management Area**	**Total**
Desert Bighorn (*Ovis canadensis*)	0	0	3	3
Red Fox (*Vulpes vulpes*)	1	0	0	1
Feral Goat (*Capra hircus*)	0	1	0	1
Total	**17877**	**13929**	**8164**	**39970**

Table 2. Environmental variables used in the CCA to investigate relationships within the mammalian communities from 3 study sites in western Texas, 2014-2015, with the corresponding CCA code and p-value. Variables were given a p-value by the CCA because of collinearity are designated by an asterisk in the p-value column.

Variable Description	**CCA Code**	**p-value**
Long-term Mean Air Temperature	MeanT	p = 1.0000
Standard Deviation of Mean Temperature	MenSdevT	p = 0.0280
Daily Minimum Temperature	SayMinT	p = 0.1538
Standard Deviation of Minimum Temperature	MinSdevT	p = 0.2208
Daily Maximum Temperature	DayMaxT	p = 0.0010
Standard Deviation of Max Temperature	MaxSdevT	p = 0.0220
Long-term Mean Precipitation	MeanPrec	p = 0.0919
Actual Precipitation	ActPrecp	p = 0.1409
Latitude	Lat	p = 0.0010
Longitude	Lon	p = 0.0010
Elevation of Camera	Elev	p = 0.0010
Elevational Change within Camera Buffer	ElevRang	p = 0.0010
Elevational Change within Study Site	Rise	p = 0.0010
Distance to Nearest Permanent Water	DistH2O	p = 0.0010
Drainage Habitat Type	drainge	p = 0.0010
Lowland Habitat Type	lowland	*
Midslope Habitat Type	midslop	p = 0.0010

Table 2, con't. Environmental variables used in the CCA to investigate relationships within the mammalian communities from 3 study sites in western Texas, 2014-2015, with the corresponding CCA code and p-value. Variables were given a p-value by the CCA because of collinearity are designated by an asterisk in the p-value column.

Variable Description	**CCA Code**	**p-value**
Upland Habitat Type	upland	$p = 0.0010$
Area of Low Canopy Class	CALow	$p = 0.0010$
Area of Medium Canopy Class	CAMed	*
Area of High Canopy Class	CAHigh	$p = 0.0010$
Number of Patches in Camera Buffer	LnumPat	$p = 0.0010$
Number of Patches of Low Canopy Class	numPatL	*
Number of Patches of Medium Canopy Class	numPatM	$p = 0.0010$
Number of Patches of High Canopy Class	numPatH	$p = 0.0010$
Mean Patch Size of Camera Buffer	mpsland	$p = 0.0010$
Mean Patch Size of Low Canopy Class	mpslow	$p = 0.0010$
Mean Patch Size of Medium Canopy Class	mpsmed	$p = 0.0010$
Mean Patch Size of High Canopy Class	mpshigh	$p = 0.0010$
Standard Deviation of Patch Size of Camera Buffer	sdland	$p = 0.0010$
Standard Deviation of Patch Size of Low Canopy Class	sdlow	$p = 0.0010$
Standard Deviation of Patch Size of Medium Canopy Class	sdmed	$p = 0.0010$
Standard Deviation of Patch Size of High Canopy Class	sdhigh	$p = 0.0010$
Total Edge within Camera Buffer	Teland	$p = 0.0010$

Table 2, con't. Environmental variables used in the CCA to investigate relationships within the mammalian communities from 3 study sites in western Texas, 2014-2015, with the corresponding CCA code and p-value. Variables were given a p-value by the CCA because of collinearity are designated by an asterisk in the p-value column.

Variable Description	**CCA Code**	**p-value**
Total Edge of Low Canopy Class	Telow	*
Total Edge of Medium Canopy Class	Temed	p = 0.0010
Total Edge of High Canopy Class	Tehigh	p = 0.0010
Edge Density of Camera Buffer	Edland	*
Edge Density of Low Canopy Class	Edlow	*
Edge Density of Medium Canopy Class	Edmed	*
Edge Density of High Canopy Class	Edhigh	*
Mean Patch Edge of Camera Buffer	MPEland	p = 0.0010
Mean Patch Edge of Low Canopy Class	MPElow	p = 0.0010
Mean Patch Edge of Medium Canopy Class	MPEmed	p = 0.0010
Mean Patch Edge of High Canopy Class	MPEhigh	p = 0.0010
Mean Perimeter-Area Ratio of Camera Buffer	MPARland	p = 0.0010
Mean Perimeter-Area Ratio of Low Canopy Class	MPARlow	p = 0.0050
Mean Perimeter-Area Ratio of Medium Canopy Class	MPARmed	p = 0.0010
Mean Perimeter-Area Ratio of High Canopy Class	MPARhigh	p = 0.0010
Shannon's Diversity	Diversty	p = 0.0010
Evenness	Evenness	p = 0.0010

Table 2, con't. Environmental variables used in the CCA to investigate relationships within the mammalian communities from 3 study sites in western Texas, 2014-2015, with the corresponding CCA code and p-value. Variables were given a p-value by the CCA because of collinearity are designated by an asterisk in the p-value column.

Variable Description	**CCA Code**	**p-value**
Month of January	Jan	p = 0.1788
Month of February	Feb	p = 0.3067
Month of March	Mar	p = 0.1269
Month of April	Apr	*
Month of May	May	p = 0.2288
Month of June	Jun	p = 0.1119
Month of July	Jul	p = 0.9111
Month of August	Aug	p = 0.1049
Month of September	Sep	p = 0.3516
Month of October	Oct	p = 0.0030
Month of November	Nov	p = 0.0210
Month of December	Dec	p = 0.1039

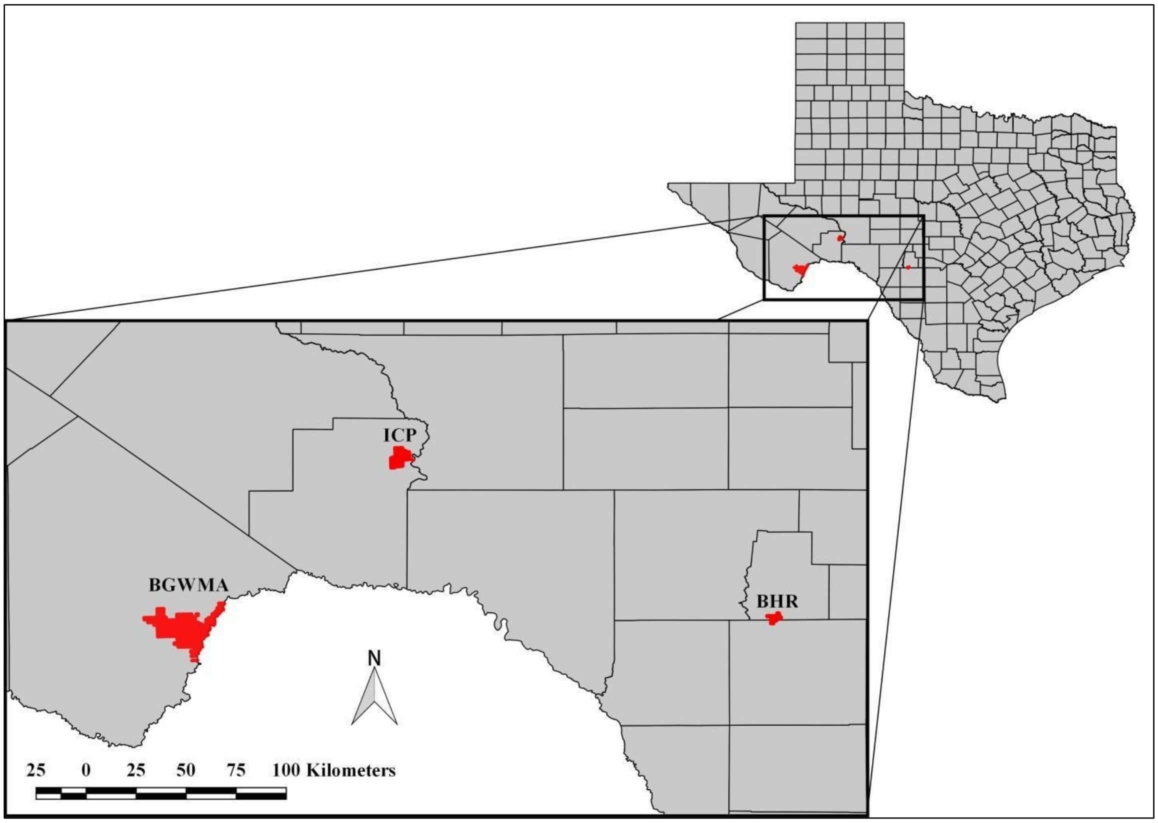

Figure 1. Location of Buckhollow Ranch (BHR), Independence Creek Preserve (ICP), and Black Gap Wildlife Management Area (BGWMA) in Texas used in exploration of mammalian community structure, 2014-2015.

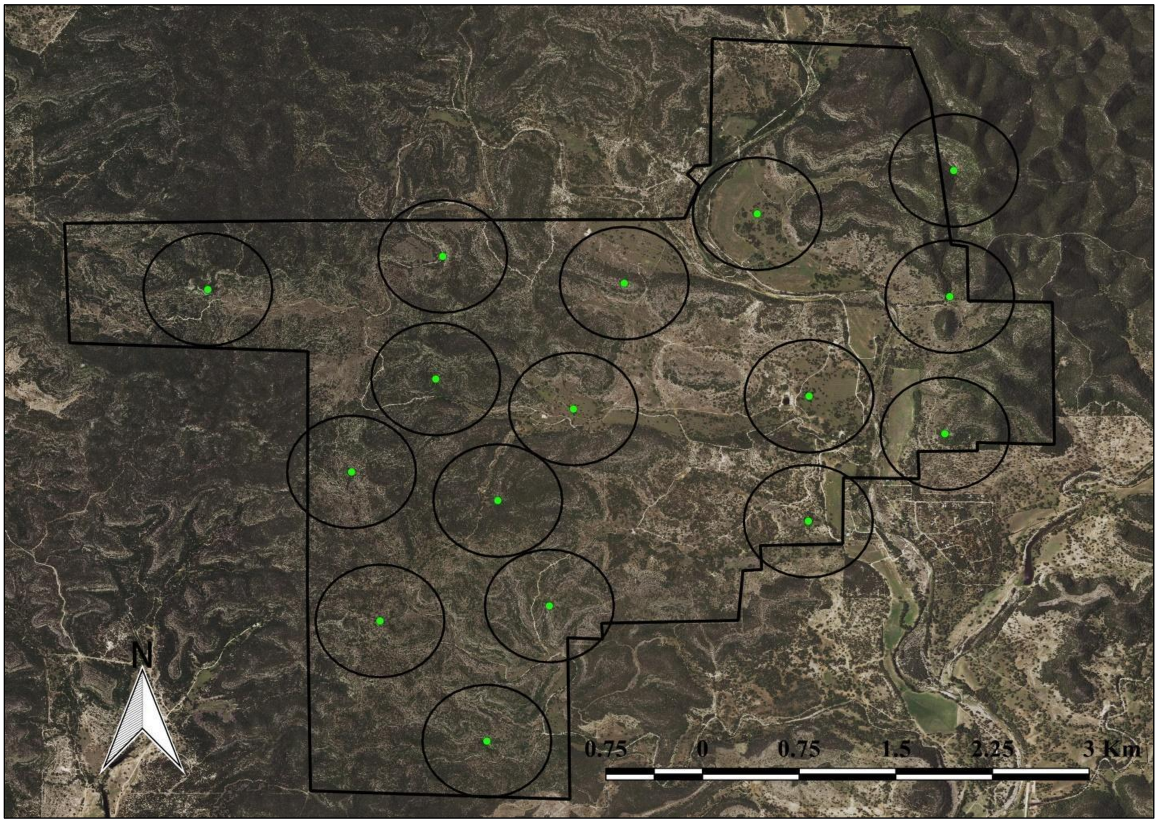

Figure 2. Location of camera traps at Buckhollow Ranch used in exploration of mammalian community structure, 2014-2015. Each camera location is surrounded by a 500 m radius buffer circle.

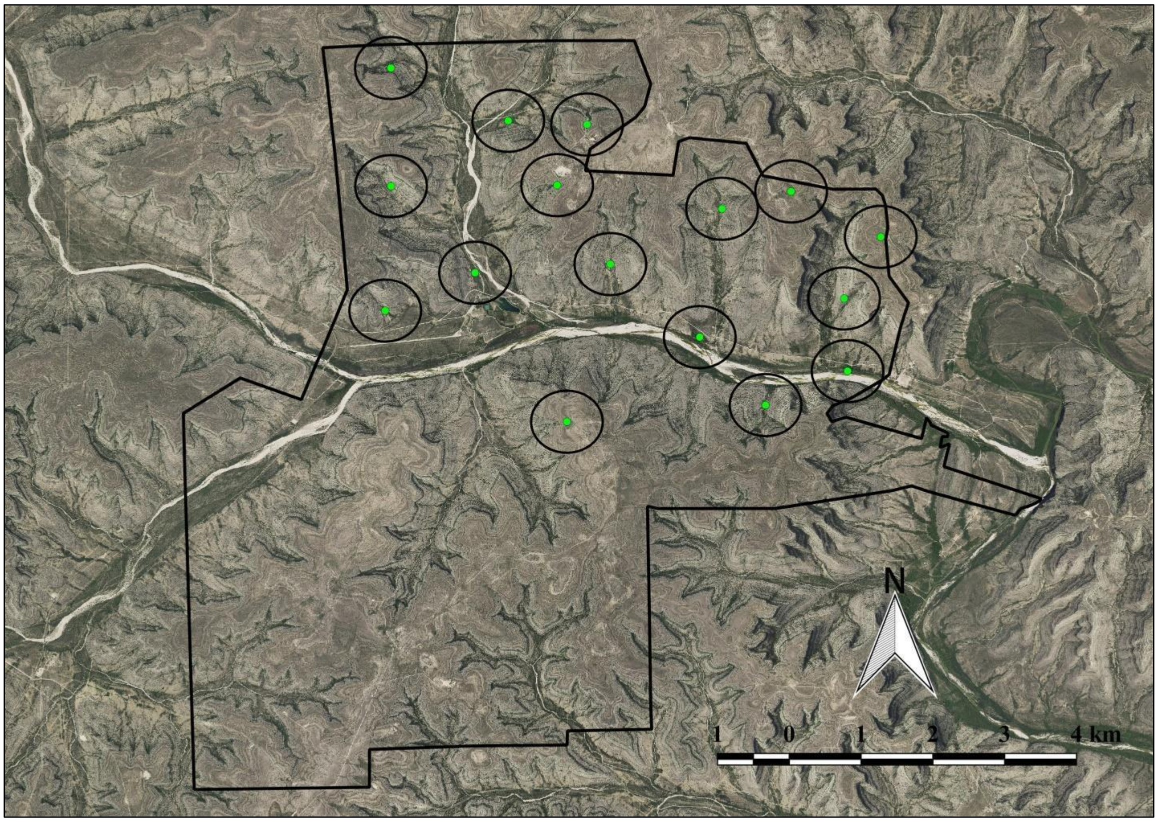

Figure 3. Location of camera traps at Independence Creek Preserve used in exploration of mammalian community structure, 2014-2015. Each camera location is surrounded by a 500 m radius buffer circle.

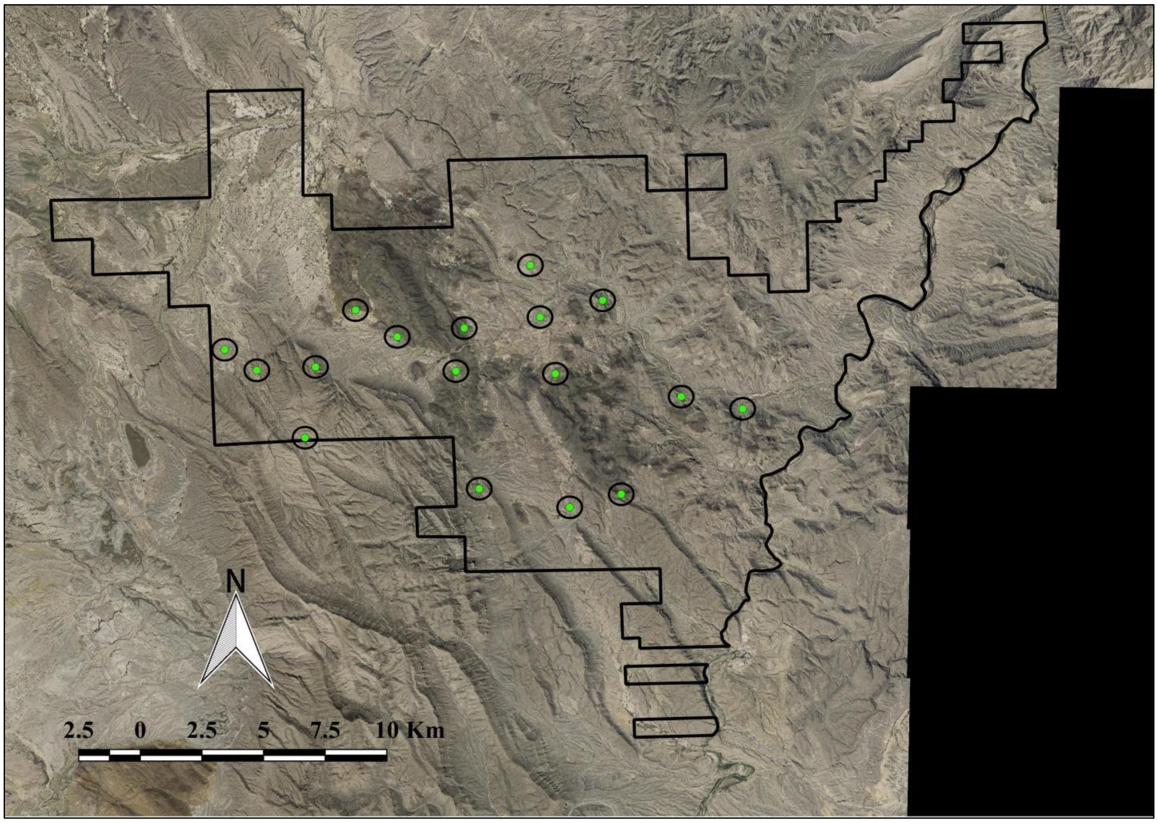

Figure 4. Location of camera traps at Black Gap Wildlife Management Area used in exploration of mammalian community structure, 2014-2015. Each camera location is surrounded by a 500 m radius buffer circle.

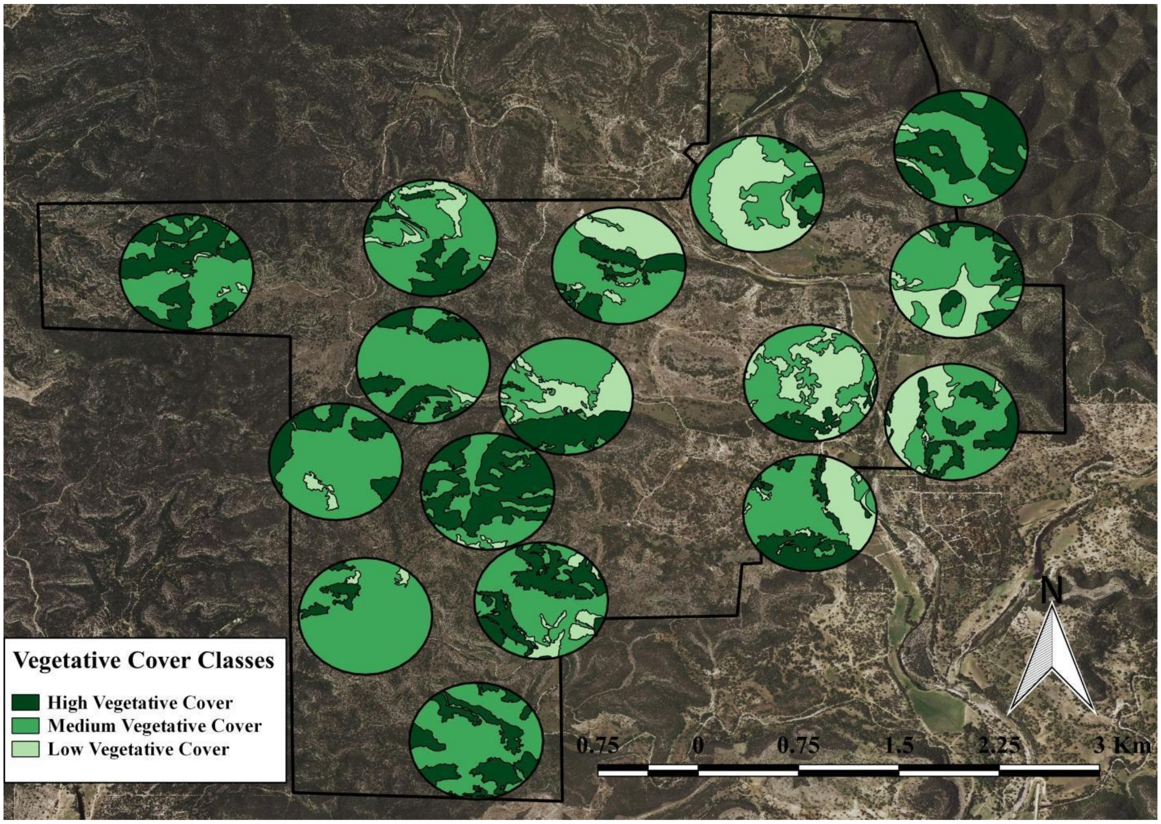

Figure 5. Example of vegetative cover class digitization within each 500 m radius camera buffer circle at Buckhollow Ranch for exploration of mammalian community structure, 2014-2015.

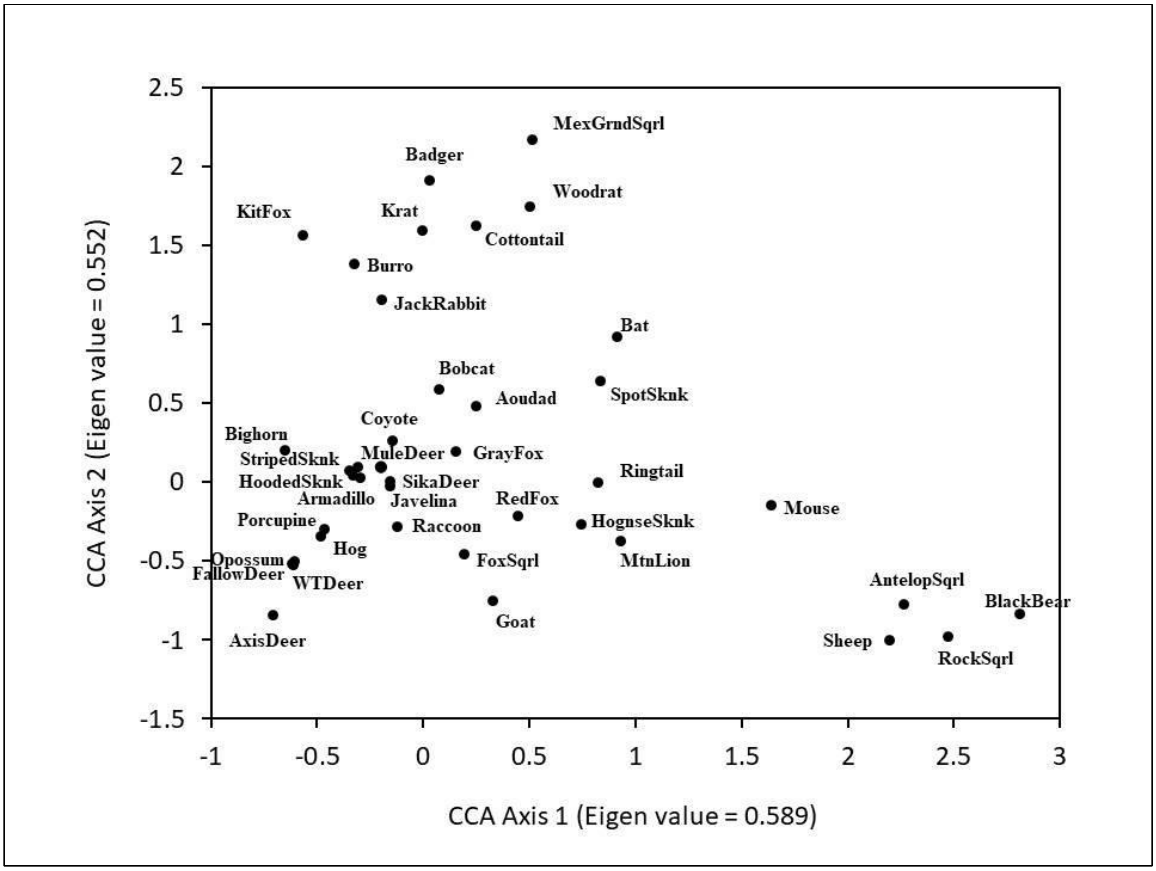

Figure 6. Species positions from Axis 1 (Eigen value = 0.589) vs. Axis 2 (Eigen value = 0.552) from the CCA using CANOCO for the study of environmental influences on species assemblage patterns of mammalian fauna at 3 sites in Western Texas.

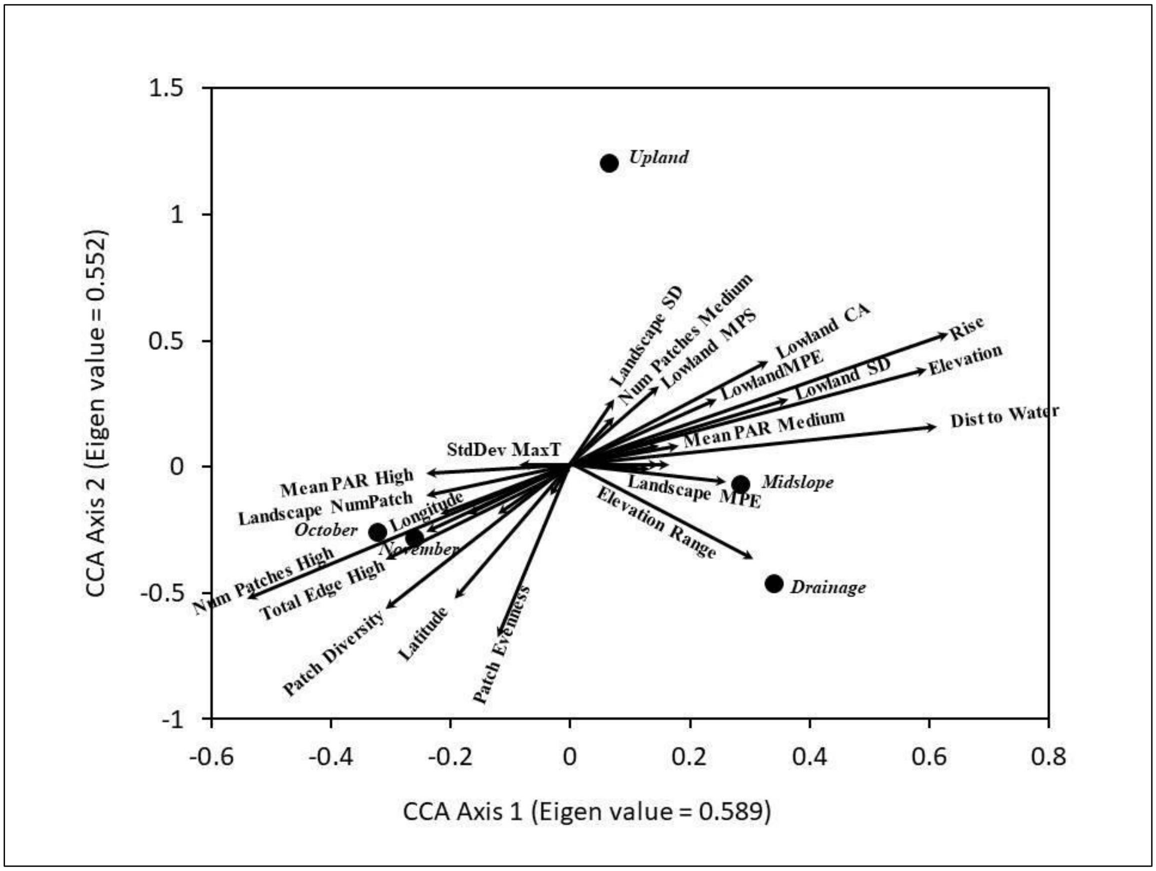

Figure 7. Environmental variable positions from Axis 1 (Eigen value = 0.589) vs. Axis 2 (Eigen value = 0.552) from the CCA using CANOCO for the study of environmental influences on species assemblage patterns of mammalian fauna at 3 sites in Western Texas.

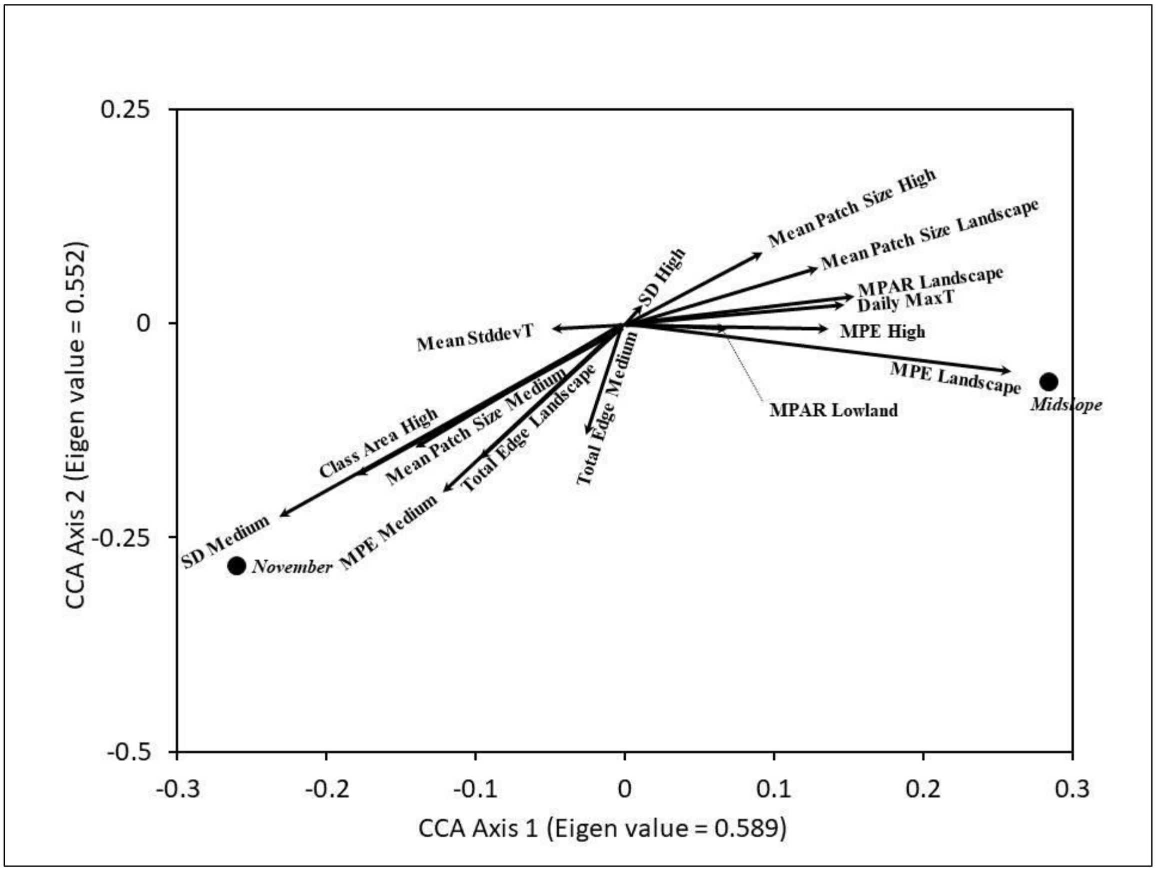

Figure 8. Zoomed portion of environmental variable positions from Axis 1 (Eigen value = 0.589) vs. Axis 2 (Eigen value = 0.552) for shorter gradients obscured in Figure 7 from the CCA using CANOCO for the study of environmental influences on species assemblage patterns of mammalian fauna at 3 sites in Western Texas.