

EXAMINING THE EFFECTS OF URBANIZATION ON OCCURRENCE OF
MAMMAL SPECIES IN NATURAL AREAS OF
THE EASTERN EDWARDS PLATEAU

by

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ABSTRACT

Central Texas is experiencing urbanization at an unprecedented rate. This anthropogenic conversion of land is due in part to a rapidly growing population in the Austin and San Antonio metro areas and the development of infrastructure and resources needed to support that growth. Urban parks, greenspaces, and preserves serve to mitigate the impact of land development by serving as habitat for local wildlife populations. To maximize the potential of this habitat, we must assess how urbanization influences species across a landscape. Mesocarnivores act as top-tier predators in an ecosystem almost completely devoid of large predators and are severely impacted by urbanization and habitat fragmentation. I surveyed 72 sites (point locations) across nine different study areas throughout the eastern Edwards Plateau ecoregion of central Texas for fourteen survey occasions during 2013. Using occupancy modeling, I examined the influence of ten different urban covariates on mesocarnivore occurrence. Generalist species, such as raccoons and opossums, had an increased probability of occurrence at sites with higher urban influence and were most likely to occur in smaller more urban study areas. Ringtails and grey foxes appeared to be unaffected by urbanization and were equally likely to occur across all sites. Results for other species, such as the coyote and skunk, were inconclusive. Most species had very low probability of detection with only the raccoon and fox having a probability greater than 0.1. Knowledge of the effect

of urbanization on wildlife could assist us in evaluating current preserves as well as devising strategies to conserve species in any planned future preserves.

I. INTRODUCTION

Background

Habitat loss and fragmentation resulting from the anthropogenic conversion of land poses one of the greatest threats to biodiversity world-wide (Crooks 2002; Tigas et al. 2002; McKinney 2006; Crooks et al. 2011; Soga and Koike 2013). Landscape-level alterations can lead to shifts in the composition and structure of biological communities (Prange and Gehrt 2004; Beasley and Rhodes 2010). Environmental alterations may be the result of natural disturbances such as grazing (Fuhlendorf et al. 2001), fire, and flood (Barbour et al. 1999; Karsai and Kampis 2011) but human-perpetuated disturbances most often result in the permanent transformation of wildlife habitat that is further compromised by a rapidly growing and urbanizing human population (Markovchick-Nicholls et al. 2006; McKinney 2006).

A multitude of anthropogenic influences can cause ecosystem alteration and loss of natural habitat due to the construction of housing, roads, utilities, agriculture, commercial and industrial development, and natural resource extraction (Riley et al. 2003; Whittington et al. 2005; Randa and Yunger 2006; Bateman and Fleming 2012). Characteristics of urbanizing areas include changes in microclimate, water availability, light intensity, ambient noise, habitat connectivity, and increased invasive species prevalence (Ghert et al. 2010). Since these effects can be far-reaching, beyond the boundaries of urban centers, the term 'urbanization' typically describes a wide array of human activities regardless of their intensity (Bateman and Fleming 2012). Also, urbanization can include the process of habitat fragmentation that occurs when

development of landscapes (by humans) causes subdivision of natural habitat into smaller patches that often experience increased isolation, increased edge effects, and higher levels of direct human disturbance (Prange and Gehrt 2004; Spinozzi et al. 2012).

Behavioral responses of wildlife species to urban development varies within and across taxonomic groups. With the spread of urbanization, many species have suffered range contraction (Tiagas et al. 2002; Bateman and Fleming 2012) while others, especially non-native species, have expanded their ranges (McKinney 2006; Veech et al. 2011). When dispersal is restricted due to habitat isolation, some animal populations may face extirpation or extinction (Markovchick-Nicholls et al. 2008; Crooks et al. 2011; Mills 2013). Species who react favorably to urbanization, urbanophiles, are typically adept in exploiting anthropogenic structures for habitation (Harrison 1997), utilizing human refuse and agriculture as a food source (Prange and Gehrt 2004;), using unpaved roads or trails for foraging and dispersal (Whittington et al. 2005), and avoiding predators that may be less inclined to venture near human habitation (Muhly et al. 2011). Urbanophobic species, those that are deterred by urbanization, may be displaced through loss of essential resources and are generally intolerant of human activity and disturbance (Prange and Gehrt 2004; Markovchick-Nicholls et al. 2008).

Wildlife residing in or near urbanized areas also face a host of other detriments such as increased competition for resources, exposure to disease, nest predation, pollution, vehicular mortality, or potentially harmful changes in demographic structure (Gehrt et al. 2010; Magle et al. 2012; Mills 2013). With an increased chance of mortality in urbanized areas and a decreased chance of recolonization or reproduction, small

habitat patches surrounded by urban areas may act as populations sinks for some wildlife species (Riley et al. 2003; Karsai and Kampis 2011). If a species is neither attracted nor deterred by urbanization, they can be considered urban neutral.

The basic life history attributes of a species might also determine whether the species is affected by urbanization. Wildlife species that have large home-ranges, occur in low densities, have low reproductive rates, are highly specialized with regard to diet and habitat, have low dispersal rates, and are susceptible to human persecution are the most likely to be affected by urbanization and fragmentation (Crooks 2002; Randa and Yunger 2006; Riley 2006; Crooks et al. 2011; Spinozzi et al. 2012). Large- and medium-sized mammals, especially carnivores, typically possess these characteristics (Musiani et al. 2010).

The extent to which mammalian carnivores are impacted by anthropogenic factors varies among species. In addition, previous research investigating mesocarnivore response to urbanization shows conflicting results within species. Occurrence of Virginia opossum (*Didelphis virginiana*) was observed by Crooks (2002) and Markovchick-Nicholls et al. (2008) to be strongly and positively correlated with proximity to urban edge, but Ordeñana et al. (2010) found that opossums occur less frequently in areas of high urban intensity. Grey foxes (*Urocyon cinereoargenteus*) were found to be positively associated with urban edges (Crooks 2002; Riley 2006), but were also observed to be negatively associated with roads (Markovchick-Nicholls et al. 2008) and intense urbanization (Harrison 1997; Ordeñana et al. 2010).

Raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), and other generalist species are well known to utilize anthropogenic food sources and shelter provided by urban and agricultural development where they may subsist in small habitat patches and have higher densities and smaller home ranges than rural populations (Bateman and Fleming 2012). Grey foxes, opossums, coyotes (*Canis latrans*), and striped skunks (*Mephitis mephitis*) have been observed eating agricultural crops (Borchert et al. 2008), but Dijak and Thompson (2000) and Hilty and Merenlender (2004) did not observe any preference given to agricultural land by the Virginia opossum. Mammals that are more likely to flourish in urban environments are generally smaller in body size, have flexible diets, and exhibit high behavioral plasticity (Crooks 2002). Larger mammals, like the bobcat (*Lynx rufus*) and mountain lion (*Puma concolor*), that have strict dietary requirements, longer dispersal distances, and are territorial tend to be more sensitive to human presence and habitat loss (Markovchick-Nicholls et al. 2008). In some cases, large predators, such as the coyote, have been observed to be positively associated with human presence (Ordeñana et al. 2010; Bateman and Fleming 2012) while in other instances, they have shown spatial and temporal displacement due to human activity (George and Crooks 2006; Gehrt et al. 2009).

Urban parks and greenspaces that are covered by habitat conservation plans mitigate incidental take of protected and sensitive species and may allow remaining patches of habitat to serve as necessary refuges for wildlife in urbanizing landscapes (Miller and Hobbs 2000; Wilhere 2002). However, continued human activity within and near these areas can compromise the intended effects (Taylor and Knight 2003; George

and Crooks 2006; Davis et al. 2010). The construction of trails, powerline corridors, high fences, roads and highways can further fragment remaining habitat and disrupt species distribution across these urbanizing areas (Papouchis et al. 2001; Tigas et al. 2002).

Studying the effects of urbanization on the occurrence of mammalian carnivores and their use of space in protected natural areas is an important step in maintaining viable populations of each species in urbanizing landscapes and can serve as a key component in wildlife management plans (Thompson 2004).

The Interstate-35 corridor stretching approximately 125 kilometers from Austin to San Antonio is one of the fastest growing regions in the country (Peralta 2014; U.S. Census Bureau 2014) (Appendix A and Map A1). San Marcos was the fastest growing city (for cities over 50,000) from 2011 – 2013 with an average annual growth of 8%. Also within the top ten fastest growing U.S. cities per capita are Cedar Park (about 30 kilometers northwest of Austin) at fourth (5.6%) and Georgetown (about 45 kilometers north of Austin) at seventh (about 4.5%). San Antonio was ranked fourth in numerical population growth (U.S. Census Bureau 2010). Loss of natural habitat from suburban and urban development is further compounded by construction of new highways, powerline corridors, and oil/natural gas exploration and associated infrastructure which all lead to fragmentation.

In addition to rapid urbanization within central Texas, considerable drought has significantly affected the entire state to the extent that in recent history, several cities were threatened with complete water loss (Combs 2012). Short-term droughts from 2000-2011 resulted in woody vegetation losses, unparalleled since the 1950s, that led to

significant damage to forests and woodlands (Twidwell et al. 2014). Although central Texas is faced with unprecedented growth of the human population, very little research has been conducted on the response of wildlife to increasing growth and urbanization. Therefore, studies investigating these dynamics could be very important in assessing how well natural areas are preserving native wildlife, especially mammalian carnivores.

Occupancy modeling

Data on the presence/absence of a focal species across multiple sites within an area of interest may be used to estimate the probability that a randomly selected site is occupied by that species (MacKenzie et al. 2006). This probability, generally referred to as occupancy (ψ), can be estimated as the proportion of occupied sites: $\psi = \frac{x}{s}$ within an area of interest where x is the number of sites occupied by a species and s is the total number of sites surveyed. When selecting variables to make inferences about habitat use or population size, consideration must be given to the most relevant characterization of the study system and the practicality of obtaining sufficient data to estimate the selected variable (MacKenzie et al. 2006; Penman et al. 2009). Estimating the proportion of sites occupied by a species of interest over a large area is considered to be much less costly in time and effort than estimating abundance (Royle and Nichols 2003; Kendall and White 2009). Therefore, occupancy modeling has become an important tool in long-term monitoring programs and metapopulation studies (Mackenzie et al. 2003; Bailey et al. 2007).

Using a flexible likelihood framework, occupancy modeling can be adjusted to accommodate covariate data for modeling habitat use and environmental heterogeneity. In addition, incorporating the parameter, p (the probability of detecting a species given its presence), allows for more robust inferences of occupancy estimates by accounting for false absences when a species has a detection probability of less than one. Within this modeling framework, maximum likelihood estimates (MLE's) are used to simultaneously estimate all model parameters (MacKenzie et al. 2006).

Accounting for imperfect detection

Two critical components of sampling animal populations are accounting for spatial variation in abundance and imperfect detectability (MacKenzie et al. 2006; Kendall and White 2009). In many cases, the study area is too large to be surveyed completely so a subsample of sites within that area may be selected in a manner (random, stratified, or other) that represents the sites not surveyed. The number of study sites and their locations within an area of interest are imperative to study design when addressing competing hypotheses and to assure the sampled population represents the true population so that accurate inferences can be made about the entire study area (MacKenzie et al. 2006). In addition, very few species can be detected perfectly; in particular, species that are cryptic, rare, or elusive will always have detection probabilities < 1 (Thompson 2004; Zabala et al. 2005). If a site is surveyed but no animal is detected, then the site is either 1) truly unoccupied; or 2) occupied but the species went undetected. When detection is not incorporated into occupancy estimates,

the naïve estimate of occupancy will be biased low. To accommodate these false absences, multiple repeated surveys of a site can be conducted during a time when the occupancy state (or “availability”) of the species is assumed constant and the probability of detecting the species at least once during K surveys is

$$p^* = 1 - (1 - p)^K$$

where p is the known probability of detecting the species in a single survey given that it is present. However, the true probability of detecting a species in a single survey is rarely known so it must be estimated by modeling the probability based on observed data (MacKenzie et al. 2006).

Single-season occupancy models

Single-season occupancy models are applied to presence/absence (1, 0) data collected over a single closed season during multiple repeat surveys of study sites, plots, transects, or points. These models have the following assumptions: 1) all sites are closed to changes in occupancy (if individuals of the species exist at the site then they are always available to be detected); 2) detection histories for each site are independent from one-another; 3) differences in occupancy and detection between sites and surveys are modeled using covariates, and 4) the target species is never misidentified (MacKenzie et al. 2002; MacKenzie et al. 2006). We can obtain estimates of occupancy (ψ) by surveying s number of sites for K distinct sampling or surveying occasions and recording the detection histories (series of 0s and 1s for a site) in a matrix where each row vector contains site-specific (h_i) presence-absence data across K sampling

occasions. For example, if a site is surveyed for three occasions and the species was only detected on the first and third sampling occasions then the detection history would be recorded as $h_i = [101]$. The probability of observing detection history $h_i = [101]$ is

$$\Pr(h_i = [101]) = \psi p_1 (1 - p_2) p_3$$

given that the site is always occupied with the probability ψ . This is the probability that the site is occupied multiplied by the probability of detecting the species in the first and third surveys and not detecting the species in the second survey. A detection history $h_i = [000]$ will have the combined probabilities of the site being occupied but not detecting the species in all three surveys in addition to the site being truly unoccupied ($1 - \psi$). After creating a probability statement for each of the i observed detection histories, the combined model likelihood can be constructed as

$$L(\psi, p | h_1, h_2, \dots, h_s) = \prod_{i=1}^s \Pr(h_i)$$

The model likelihood can then be maximized using maximum likelihood estimators to simultaneously estimate the parameters for occupancy and detection probability (MacKenzie and Bailey 2004; MacKenzie et al. 2006).

Modeling covariates

The probability that a particular site is occupied by a given species is ultimately a function of patch characteristics such as size, geographic location, and habitat composition of the patch and surrounding landscape (MacKenzie 2006; Long et al. 2011; Collier et al. 2012). The probability of detecting a species may also be a function of

measureable variables such as habitat type, time of day, weather conditions, and observer identity (MacKenzie et al. 2002). To account for heterogeneity in occupancy and detectability across sites and surveys, both parameters can be modeled as a function of covariates using the general multiple logistic equation

$$\theta_i = \frac{\exp(X_{ij}\beta_j)}{1 + \exp(X_{ij}\beta_j)}$$

where θ_i can represent either ψ or p for site i , X_{ij} is the covariate value for site i and covariate j and β_j is the regression coefficient to be estimated for covariate j . If occupancy estimates are site-specific according to their covariate values, then the estimates can be averaged across all sites (or a subset of sites) by

$$\bar{\psi} = \frac{\sum_{i=1}^s \psi_i}{s}$$

A sampling “season” refers to a period of time at which the probability of a species occupying a site remains constant, or the site is said to be closed. The assumption of site closure will be violated if the occupancy state of a species at any site changes due to non-random processes. Because a “site” is defined at a spatial scale where the assigned 1 or 0 (presence-absence) is meaningful, then the definition of a season may vary depending on the size of a site (MacKenzie et al. 2006). If the objective is to determine if a site is “occupied”, then the species must be present for the entire duration of the sampling season. If a species occurs at a site intermittently during a season, then it may be more appropriate to interpret the site as “used” (MacKenzie 2006; MacKenzie et al. 2006; Longoria and Weckerly 2007) rather than permanently occupied. Regarding my study and its design (see Methods section), I will refer to use of

sites rather than strict occupancy and use the term “probability of occurrence” across a set of sites.

Model selection and assessing fit

Applying an information-theoretic approach allows for comparison of multiple models representing competing hypotheses and selection of the “best” model from that set (Burnham and Anderson 2002; Gotelli and Ellison 2004). This approach uses the principle of parsimony to compare the tradeoff between bias and variance explained by the model. Adding more parameters to a model can decrease the bias but at the same time increase the variance of parameter estimates (Burnham and Anderson 2002; MacKenzie et al. 2006). During model selection, Akaike information criterion (AIC; Burnham and Anderson 2002) values of models are evaluated and compared; the lowest AIC value typically represents the model with the fewest parameters that fits the dataset the best. If two or more models have similar AIC weights (w) such that $\Delta AIC < 2$, then parameter estimates of these models can be used to get weighted average estimates (Burnham and Anderson 2002; Thorn et al. 2009; Lazenby and Dickman 2013). If the sample size is small in comparison to the number of parameters being estimated ($n/K < 40$), models can be ranked using AIC_c , which adds a small sample bias-correction term (Burnham and Anderson 2002). However, just because one (or more) particular model(s) is selected as the best does not mean it is a good model (MacKenzie et al. 2006). Even the “best” model might not always adequately fit the data. MacKenzie and Bailey (2004) describe a method of assessing fit of occupancy models by comparing

observed detection histories to those expected if the model is assumed to be accurate. Their method uses a Pearson's chi-square test in which model fit is determined based on the value of the calculated X^2 test statistic calculated over all the recorded detection histories. Bootstrapping can be utilized to determine if any of the observed histories are unusually large. An overdispersion parameter, \hat{c} , is calculated as

$$\hat{c} = X_{Obs}^2 / \bar{X}_B^2$$

where \bar{X}_B^2 is the average chi-square value from the parametric bootstraps and X_{Obs}^2 is the value obtained for the actual observed data (detection histories). If \hat{c} is near 1, then the observed and expected detection histories match one another and the model is determined to sufficiently fit the data. If the most inclusive model (model with the highest number of parameters) is poorly fit, then the \hat{c} value can be used to adjust standard errors in order to make more accurate inferences of parameter estimates (Burnham and Anderson 2002).

Purpose

The goal of my study was to identify anthropogenic factors that affect the probability of occurrence by large- and medium-sized mammals, specifically mesocarnivores. Using presence/absence data collected by motion-activated cameras, I sought to accomplish two main objectives: 1) Examine relationships between sources of urban influence and occurrence of various mammal species in the study areas; and 2) Compare how mesocarnivore occurrence varies across study regions.

A comparison of mesocarnivore habitat use across various parks, greenspaces, and preserves in the Texas Hill Country can give insight into how different magnitudes of urbanization impact top-trophic-level species and potentially, ecosystem dynamics. The results from this study can be used for future land management decisions and assessing the success of habitat conservation plans. In addition, some mesocarnivore species, specifically the ringtail (*Bassariscus astutus*), are understudied and obtaining basic population information for these species is particularly valuable. Furthermore, collecting baseline data on mesocarnivore distribution in central Texas is imperative to the proper management of wildlife in a rapidly urbanizing environment. If presence/absence data is collected over time, multi-season occupancy models can be used to estimate colonization and extinction rates from large-scale and long-term monitoring programs, monitor the spread of invasive species (e.g., feral pigs (*Sus scrofa*)), and assess the success of management programs aimed at reducing populations of superabundant species (e.g., white-tailed deer (*Odocoileus virginianus*)).

Central Texas also encompasses the breeding ground of the federally endangered Golden-cheeked warbler (GCWA; *Dendroica chrysoparia*) and Black-capped vireo (BCVI; *Vireo atricapilla*) and several parks and preserves in Texas were created with the intent to mitigate the impact of development on these birds. Because some mesocarnivore species such as raccoons, ringtails, and gray foxes, are known to act as nest predators (Miller and Hobbs 2000; Conkling et al. 2012) and may persist in high densities near urban areas (Riley 2006), determining exactly how these species respond

to anthropogenic factors can be beneficial to conservationists when selecting potential preserve sites for GCWA and BCVI or determining acceptable land use within a preserve.

Extensive literature exists demonstrating the ability of generalist mesocarnivore species to adapt, and even thrive, near urbanized areas (Prange and Gehrt 2004; Randa and Yunger 2006; Markovchick-Nicholls et al. 2008; Ordeñana et al. 2010). Based on this information, I expect habitat use (probability of occurrence) of opossums, raccoons, ringtails, and skunks to increase with proximity to urban areas and with high levels of anthropogenic influence. In light of conflicting research regarding effects of urbanization on coyotes and grey foxes, I predict that occurrence of these species will remain relatively constant across all sites due to their ability to travel great distances within and between urban and rural landscapes. I also predict that specialist species, such as the mountain lion and bobcat, will be deterred by human presence and will be less likely to occur near urban development or in study areas smaller than their average home range size. In addition, I hypothesize that species who maintain large home ranges and low densities will be less likely to be detected and will have lower overall estimates of ψ .

II. METHODS

Camera-trapping

Camera-trapping via the use of automatic motion-activated cameras is becoming increasingly popular in collecting presence/absence data on low-density, rare, or elusive mammal species (O'Connell et al. 2011; Hamel et al. 2013). Digital mass storage of media, reduction in size, more efficient batteries, and lower monetary costs now allow long survey periods to be conducted without having to frequently check the status of remote camera-traps. The development and evolution of powerful statistical techniques has led to new applications of camera trap data (O'Connell et al. 2011). In addition to selected target species, camera surveys using passive camera systems (motion- and/or infrared-triggered) can also collect substantial data on non-target species (Kelly and Holub 2008).

Study areas

I used motion-activated cameras to collect presence-absence data for mammalian carnivores at 72 sites within nine study areas along the eastern boundary of the Edwards Plateau in central Texas (Appendix A, Maps A1 - A7). All study areas are located roughly between San Antonio and Austin and, with the exception of McKinney Falls State Park, are within the Edwards Plateau ecoregion. The Edwards Plateau ecoregion is characterized by temperate shrublands, savannahs and grasslands with shallow soils covering limestone bedrock. McKinney Falls State Park is located a few miles east of the Edwards Plateau, in the Blackland Prairies ecoregion which is

characterized by deep clay soils, tallgrasses (historically), and dissected by riparian woodlands. Study areas differed in a wide variety of attributes such as size, use, and extent of surrounding urban impact. The study areas included Purgatory Creek Natural Area (PCNA), Ringtail Ridge Natural Area (RRNA), and Spring Lake Natural Area (SLNA) in San Marcos; McKinney Falls State Park (MFSP) in south Austin; the South Lake Austin Macrosite (SLAM) and Upper Bull Creek Macrosite (UBCM) of west suburban Austin; Pedernales Falls State Park (PFSP) near Johnson City; and the Balcones Canyonlands National Wildlife Refuge (BCNWR) northwest of Marble Falls (see Appendix B for detailed description of each study area).

Site selection in GIS

I used ArcMap 10.1 (ESRI, Redlands, CA) to create a work environment for all GIS spatial analysis of study areas and surrounding landscapes. Aerial imagery (from 2012) and Texas public road layers were obtained from the Texas Natural Resource Information System (www.TNRIS.org). GIS files for study area boundaries, trails, and roads were obtained from the respective ownership or administrative organization. Land cover raster data was obtained from the National Land Cover Database (NLCD 2006, www.mrlc.gov). Before analysis, all layers were projected into UTM Zone14 from the WGS 84 datum.

In a new geodatabase, I created a raster mosaic dataset to serve as a base map and used aerial imagery of each county that contained all or part of a study area. The dataset was added using the previously mentioned coordinate system and footprints

were built to reduce the amount of empty space resulting from overlapping images. Study area polygons (depicting boundaries) and their respective trail and road layers were added as feature datasets. Depending on accessibility and available infrastructure of each study area, available sampling locations (for deploying cameras) were chosen within buffers extending 400 m from any road or trail that could be accessed by car, bike, or foot. This was to ensure deployment was logistically feasible and relatively rapid. I randomly generated 72 points (here on referred to as study sites) using Geospatial Modeling Environment (Hawthorne 2014, www.spatial ecology.com) and inserted them into ArcMap. Study sites were at least 400 m apart to ensure sampling independence based on the average home range of smaller mesocarnivores. The number of sites per study area (Appendix A, Maps A2 – A7) was based on size and feasibility of setting up camera stations in one or two days at each study area. Some study areas required that special conditions be met in order to allow research activity. Property staff reviewed locations of study sites to avoid protected/sensitive areas. Sampling at BCP study areas in the west Austin study region (SLAM and UBCM; Appendix A, Map A7) was prohibited within 100 m from houses.

Camera station configuration

Randomly selected sites within each study area were located using a handheld Garmin Montana GPS unit. In some cases, site access proved difficult due to dense vegetation, steep bluffs, or lack of access by trails so camera stations were located as close as reasonably possible to randomly generated points. All camera locations were at

least two meters from any man-made trails or roads to reduce the chances of encounter/theft by park visitors. Camera stations were created by using one Wingscapes Birdcam 2.0 (EBSCO Industries, Calera, AL) in combination with two scent lures. Using bungee cords or straps, cameras were positioned approximately 0.5 – 1 m off the ground (attached to trees) and 1 – 5 m from a scent station. Scent stations were baited using two different scent lures to attract a broad spectrum of target species into the camera's field of view. For larger predators, such as gray fox, bobcat, and coyote, I used Caven's Gusto (Minnesota Trapline Products, Pennock, MN) and for smaller mesocarnivores such as raccoons and opossums, I used Murray's Creek Walker (Murray's Lures and Trapping Supplies, Walker, WV). Each scent was applied to a swath of cotton fabric and zip-tied to its own three-sided aluminum tent stake which were then placed 15 – 30 cm apart. Cameras were left at study sites to continuously run for seven days with each 24-hour day serving as a sampling occasion. Since study areas varied greatly in size and location, cameras were most often deployed at one or two areas over the course of a weekend, retrieved the next weekend, and redeployed at a different study area(s) the following weekend so that a complete sampling "season" for all study areas typically occurred over the course of eight weeks.

Because data were collected at each site within a relatively short time span (seven days), I believe the assumption of site closure was met. That is, during 7-day period, any detected individual probably remained near enough to the camera station to be "captured" or photographed during any 24-hour period. Time stamps on the photographs enabled distinction between each day. A 24-hour day was chosen to serve

as a single sampling occasion because it corresponds well to mammal activity patterns and behavior. Also, sampling occasions require detection to be constant unless accounted for by covariates so including daytime and nighttime periods within each occasion allows for the inclusion of heterogeneity in activity.

In order to capture possible seasonal variation in mammal behavior and activity (as this could affect detection and occupancy estimates – see next section), each study area was sampled for at least two seasons (or sampling periods) of the year. Camera stations operated in the first period from 6 October through 12 November 2012 at 51 sites; in the second period from 26 January through 24 March 2013 at 71 sites; in the third period from 7 September through 25 October 2013 at 71 sites; and in the fourth period from 9 through 17 February 2014 at 34 sites. The first sampling period was used only as a preliminary investigation to test out the cameras and to ensure that the survey protocol would generate enough data for analysis. There were a few missed sampling occasions, typically a result of camera malfunctions such as continuously triggering every few minutes when sensitivity was set on high. Some cameras also just stopped working, had the flash stop working, had batteries die, and had memory cards fill up.

Calculating covariates

Covariate data were derived for each site and study area using ArcMap 10.1. Given the wide variety of target species, their varied responses to anthropogenic influences, and the numerous factors that can be classified as “urbanization”, I decided to analyze a large number of covariates to thoroughly test the effects of urbanization. A

list of all possible covariates and their descriptions is provided in Appendix C. Land cover classes of the NLCD 2006 dataset were grouped into three categories: urban, altered, and natural. Urban land cover included developed land of low, medium and high intensity (impervious surface over 20%). Altered land cover included developed open space (impervious surface less than 20%), crop land, and pastures. Natural habitat included all forests, shrublands, wetlands, and grasslands.

Because some of the land surrounding study sites had been developed since the NLCD 2006 dataset was created, I reclassified some of the 30x30 meter NLCD cells (pixels) based on more recent (2013) satellite imagery obtained from Google Maps. This was done in ArcMap by clipping a portion of NLCD raster data surrounding a study area and laying a polygon feature, known as a fishnet, over the NLCD raster that matched exactly in number of row and column cells and cell size. I then assigned cell values of the fishnet that matched the NLCD cover classes and edited those values based on changes in land cover since 2006 or for cells that appeared to be mislabeled. Large bodies of water (e.g., Lake Austin) were considered inaccessible to wildlife and were labeled as “no data” and excluded from computation. All fishnets were then converted into raster datasets for further analysis.

Land cover was calculated within 400 and 800 m radius circular buffers surrounding each site (camera station) using the ‘Tabulate Area’ tool in ArcMap. Using Microsoft Excel, I combined cover area calculations from ArcMap into their respective new cover categories (urban, altered, and natural) and determined the proportion of each category within the site buffers. Because both altered and urban cover categories

were rare and usually present in very small proportions, I changed the proportion measurements for each buffer to either containing urban or altered land cover (1) or not (0).

Trail and road densities were obtained by clipping those features to buffered areas, summing total lengths within the buffer (meters) and dividing by total land area (hectares) within the buffer. Trail and road shape files were compared to aerial imagery and personal observations and any missing segments were digitized using the editor tool in ArcMap. Lines classified as “trls” included all single- and double-track trails, private drives over 200 meters, power-line corridors, gravel roads, jeep roads, and unpaved maintenance roads. Lines classified as “rds” included all public paved roadways. Distances from nearest road (“nearrd”), trails (“neartrl”), and human habitation (“nearhab”) to each camera station were calculated using the ruler in ArcMap. Habitations were identified using 2013 satellite imagery. Structures classified as a human habitation included houses and office buildings but attempts were made to exclude barns, shacks, and other edifices where human activity might occasionally be present.

In addition to the site-specific covariates described above, I also used covariates specific to each study area. “Area” (hectares) was calculated as the area within park boundaries (see Appendix A) plus any connected natural habitat extending two kilometers outside the legal park boundary. The intent was to derive an estimate of effective size of study area from the perspective of a mesocarnivore that obviously does not recognize park boundaries. Two kilometers was chosen because it sufficiently covers

the large home range of coyotes (Riley et al. 2003). Total area did not include any non-natural land cover outside of park boundaries. In San Marcos, two kilometer buffers from two study areas (RRNA and SLNA; Appendix A, Map A2) overlapped and therefore total area was the combined area.

The last covariate, “3km”, described the urban intensity for each study area. This was calculated by buffering each study area by three kilometers and measuring the proportion of urban land cover within the entire buffer, including the study area itself. This covariate takes into account the size of the study area as well as the surrounding urbanization. The three study areas in San Marcos (PCNA, SLNA, and RRNA) and the two in west Austin (SLAM and UBCM) overlapped in their buffers so for each region, the buffers were dissolved into one and the “3 km” urban covariate was calculated across the dissolved buffer.

When developing the occupancy models, covariate data corresponding to 400 meter buffers were used in analysis of species with small body size (raccoon, opossum, ringtail, striped skunk, and cottontail rabbit) whereas larger-bodies species (grey fox and coyote) were assigned covariate data from the 800 meter buffers to reflect potential habitat use at a larger spatial extent. In addition, for the grey fox models I only used sites (camera stations) that were separated by at least one kilometer within each study area and for the coyote models I only used sites separated by at least 1.5 kilometers. This was done to reduce the amount of spatial overlap of 800 meter buffers and thus to avoid excessive spatial autocorrelation and non-independence of the data from each site.

Occupancy modeling in program PRESENCE

All occupancy modeling was conducted using the program PRESENCE v6.2 (Hines 2006) and all continuous covariate data were standardized in PRESENCE before analysis. Following conventional protocol, I first tested the effects of several covariates on detection probability. Typically, estimates of occupancy can be improved by accounting for variables (through the use of covariates) that might cause heterogeneity in detection probability. Using detection data from the only two seasons that had complete sampling (sampling periods 2 and 3) I examined possible covariate effects of Julian date, temperature, and precipitation on detection probabilities for each species. Using AIC_c , I compared all possible candidate model combinations (six models for each species) and the null model (no covariates). For all species, the null model was ranked highest without any of the covariate models being within 2 AIC_c points. Therefore, in the occupancy models (explained below) I did not use any covariates for detection probability.

Because my only focus was to examine how urbanization influences habitat use by mesocarnivores, I decided that multi-season models would be inappropriate and unnecessary. Multi-season occupancy models are used to estimate the colonization and extinction rates of sites between seasons plus the initial occupancy state and the probability of detection. This is of greater interest to metapopulation studies and long-term monitoring programs that focus on site occupancy changes over time (MacKenzie et al. 2003). Using extended survey periods in which the occupancy state of a site may

change during the course of the survey may lead to poor inferences of occupancy probabilities. However, extended survey periods may be most necessary when targeting cryptic species with low probability of detection. In addition, more parameters would have to be calculated for each colonization and extinction probability between seasons leading to heavily parameterized models with potential for highly biased parameter and covariate estimates, especially given our small sample sizes and low detection probabilities. The use of single-season models over extended survey periods does however lend itself well to interpreting site use instead of occupancy.

I created single-season occupancy models using data from sampling periods 2 and 3 so as to examine covariate effects (i.e., urbanization) on the use of space (occupancy) within each study area. As previously mentioned, due to the study design, the models are most appropriately viewed as estimating use or occurrence rather than actual occupancy per se. Because of substantial correlation ($-0.5 < r < 0.5$; Tables 1 and 2) between many of the covariate variables, all modeling was limited to single covariate models, in addition to the null models (no covariates for occupancy). Further, the main goal of the study was not to find or construct a single best comprehensive model for predicting mammal occurrence but rather to thoroughly test a wide array of landscape urbanization variables for their influence on mammal occurrence. Using typical home range size to determine appropriate spatial distance between sites, sample sizes were $N = 72$ for the raccoon, opossum, striped skunk, and cottontail rabbit occupancy models, $N = 64$ for the ringtail models (sites at MFSP were omitted since the species is less likely to

occur east of the Edwards Plateau (Schmidly 1994)), $N = 49$ for the grey fox models, and $N = 38$ for the coyote models.

For each species, I used the set of 10 single-covariate models and the null model to derive an “urbanization effect” score. This score is calculated as the sum of the standardized partial regression coefficients (beta values for the covariate in each model) adjusted by model weight and multiplied by either + 1 or - 1 if the response was positively or negatively related to urbanization. The weighted y-intercept (from the null model only) was inverse sign-adjusted and added to the summation to serve as a “penalty” by directing the score towards zero. This ensured that model sets with heavily-weighted null models would have scores that lean towards a neutrality (score = 0). Scores $\ll 0$ indicated a negative effect of urbanization on species occurrence (or space use) across all sites and scores $\gg 0$ indicated a positive effect of urbanization. Scores near zero indicated a neutral (or inconsistent) effect.

Estimates of site use (determined as weighted means over the best supported models, $\Delta AIC_c < 2$) were calculated for each species in each survey region (group of one or a few study areas) to determine if occurrence varied across regions within and among species. If the null model had $\Delta AIC_c < 2$ then estimates of ψ were derived from the null model only. If species occurrence varied from region to region then sources of urbanization (i.e., model covariates) were evaluated to determine the primary causes of heterogeneity and to pin-point the most substantial influences on species occurrence. However, if the regional occurrence of a species did not vary, only varied slightly, or varied in a manner inconsistent with urban covariate influence then that species was

determined to be unaffected by urbanization and equally likely to use all sites across the study areas. Regional estimates of occurrence were compared among species in an attempt to identify responses to urbanization based on biological attributes of the species.

III. RESULTS

There were thirteen sites with at least one missed sampling occasion in the first sampling period, four in the second, three in the third, and two in the fourth. A total of 1,452 sampling days resulted in the detection of 21 mammal species including ten mesocarnivore species [northern raccoon, Virginia opossum, grey fox, ringtail, coyote, bobcat, striped skunk, eastern spotted skunk (*Spilogale putorius*), domestic dog (*Canis lupus familiaris*), and domestic cat (*Felis catus*)]. Other mammals included white-tailed deer (*Odocoileus virginianus*), nine-banded armadillo (*Dasypus novemcinctus*), feral pig (*Sus scrofa*), collard peccary (*Pecari tajacu*), eastern fox squirrel (*Sciurus niger*), rock squirrel (*Spermophilus variegatus*), eastern cottontail (*Sylvilagus floridanus*), North American porcupine (*Erethizon dorsatum*), human, an unidentified rodent, and an unidentified goat. Large predators and mesocarnivores that were not detected but are known to occur within the Edwards Plateau included the mountain lion, red fox (*Vulpes vulpes*, non-native), long-tailed weasel (*Mustela frenata*), American mink (*Mustela vison*), American badger (*Taxidea taxus*), hog-nosed skunk (*Conepatus leuconotus*), and western spotted skunk (*Spilogale gracilis*) (Schmidly 1994).

Seven species had a naïve occupancy estimate ($\psi = \frac{x}{s}$) of 0.1 or greater and were selected for further analysis. These included the raccoon, opossum, ringtail, striped skunk, grey fox, coyote, and cottontail rabbit. Naïve estimates of occupancy for the striped skunk showed high variation between sampling periods with only the spring period having a naïve estimate > 0.1. Therefore, only the seven day period in Spring 2013 (sampling period number 2) was used for the striped skunk and the fourteen days

of periods 2 and 3 for the other species since those periods had the most complete survey histories. Because only the spring sampling period was used for the striped skunk, two sites that experienced camera malfunctions were excluded giving a sample size of $N = 70$.

Covariate data varied at the site-level and by study area. In the 400 m buffered areas road density ranged from 0 – 56.3 m/ha, trail density from 8.4 – 107.9 m/ha, and proportion of natural land cover from 0.6 – 1.0. For small mammal models, distance to nearest human habitation ranged from 31.8 – 2,247.9 m, distance to nearest trail from 2.7 – 290.5 m, and distance to nearest road from 8.3 – 3,341.9 m. In the 800 m buffered areas road density ranged from 0 – 56.2 m/ha, trail density from 3.7 – 82.1 m/ha, and proportion of natural habitat from 0.5 – 1. For large mammal datasets, distance to nearest human habitation ranged from 62.5 – 2,192.9 m, distance to nearest trail from 2.7 – 290.5 m, and distance to nearest road from 8.3 – 3,341.9 m. At the study area-level, accessible habitat area ranged from 446.8 – 53,398.5 ha and urban-intensity within 3 km of the study area ranged from 0.0006 – 0.3.

Covariates affecting probability of use

Raccoon site use was most strongly and negatively influenced by the proportion of natural habitat within 400 m ($\beta' = -6.83$, $SE = 4.24$; Figure 1) which garnered over 99% of the model set weight (Table 3). The average probability for use of any site ($\bar{\psi}_{site}$) was 0.49 ($\overline{SE} = 0.08$), 29% greater than the naïve estimate (0.38). The probability of site use ranged from 0.18 -1.00. Average estimated probability of study region occurrence for

the raccoon was greatest at McKinney Falls (MF) ($\bar{\psi}_{\text{region}} = 0.99$, $\overline{SE} = 0.02$) and least at Balcones Canyonlands (BC) ($\bar{\psi}_{\text{region}} = 0.24$, $\overline{SE} = 0.09$).

Opossum site use was positively influenced by the presence of urban land cover within 400 m ($\beta' = 2.31$, $SE = 0.96$; Figure 2), negatively influenced by the proportion of natural land cover within 400 m ($\beta' = -3.78$, $SE = 2.18$; Figure 3), and positively influence by presence of altered land cover within 400 m ($\beta' = 1.86$, $SE = 0.77$; Figure 3) for a combined total of 79% of the model set weight (Table 4). The weighted average (over all models) probability of an opossum using any site was $\bar{\psi}_{\text{site}} = 0.27$ ($\overline{SE} = 0.09$), which was 50% greater than the naïve estimate (0.18). Probability of site use ranged from 0.11 - 0.59 and opossums were approximately 4 times more likely to use urbanized sites than non-urbanized sites and 3.77 times more likely to use sites with access to altered landscapes. Average probability of study region occurrence for the opossum was greatest at MF ($\bar{\psi}_{\text{region}} = 0.53$, $\overline{SE} = 0.13$) and least at BC ($\bar{\psi}_{\text{region}} = 0.12$, $\overline{SE} = 0.04$).

Probability of coyote site use was most influenced by study area urban intensity ($\beta' = 24.21$, $SE = 21.09$; Table 5). Estimates of coyote site use were not interpreted since many site-specific standard errors were either greater than the estimate or equal to zero but the naïve estimate of the proportion of sites used by coyotes was 0.32.

Ringtail and grey fox occurrence were not strongly influenced by any of the predictor covariates (Tables 6 and 7 respectively), or at least none of the predictors explained ringtail and fox occurrence better than the null model. The probability of use across all sites for the ringtail and grey fox was $\psi = 0.49$ ($SE = 0.15$) and $\psi = 0.72$ ($SE =$

0.08) and were 81% and 11% larger than the naïve estimates (0.27, 0.65) for the ringtail and fox respectively.

No reliable model was selected for the striped skunk given that the best covariate (distance to nearest trail) had a standard error more than two times greater than its coefficient estimate. The naïve probability of occurrence for the striped skunk was 0.15.

In addition to the six mesocarnivore species previously described, the eastern cottontail rabbit also frequented camera stations. Cottontail occurrence was most influenced by the size of the study area ($\beta' = -1.17$, $SE = 0.72$; Figure 4) whose model consisted of > 39% of the model set weight (Table 8). Average probability of use across all sites was $\bar{\psi}_{\text{site}} = 0.28$ ($\overline{SE} = 0.10$) which was 56% greater than the naïve estimate (0.18). Average probability of cottontail occurrence was greatest at MF ($\bar{\psi}_{\text{region}} = 0.41$, $\overline{SE} = 0.13$) and least at BC ($\bar{\psi}_{\text{region}} = 0.03$, $\overline{SE} = 0.05$).

While some species (raccoon and cottontail) clearly had heavily weighted models, other species (ringtail, opossum, fox) did not but rather had multiple competing models that indicated the possibility of numerous sources of urbanization influencing site use. Urban effect scores indicated that the raccoon and opossum both had strong positive responses to urbanization (Table 9). Ringtails, foxes, and cottontails all displayed neutral or inconsistent responses to urbanization. Skunks and coyotes failed to produce a model set with sufficient precision in their parameter estimates to utilize this scoring method (Table 9).

For some species, mean occurrence varied among study regions (Figure 5).

Overall, raccoon occurrence and opossum occurrence were substantially greater in the smaller and more highly urbanized study regions (SM and MF) and least at the largest and less urbanized regions (SA, JC, and BC). Fox occurrence and ringtail occurrence were constant across all study regions which is due to occurrence being derived from the null occupancy model for each species. Cottontail occurrence varied slightly across regions with the exception of BC, where it was substantially lower (Figure 5).

Number of survey days needed

The probability of detection for each species during any given survey was:

raccoon = 0.11 (SE = 0.02), opossum = 0.09 (SE = 0.03), ringtail = 0.06 (SE = 0.02), grey fox = 0.17 (SE = 0.07), striped skunk = 0.04 (SE = 0.01), coyote = 0.07 (SE = 0.02), and cottontail rabbit = 0.08 (SE = 0.03) (Table 10). Using the equation $K = \log_{(1-p)}(1-0.95)$ where p is the model-estimated detection probability, the number of survey days needed to be $\geq 95\%$ certain the species is detected if present would be 26, 36, 49, 17, 72, 42, and 36 for the raccoon, opossum, ringtail, grey fox, striped skunk, coyote, and cottontail respectively (Fig 6).

IV. DISCUSSION

Effects of urbanization on mammal occurrence

Model rankings and the calculated urbanization scores for each species mostly corresponded to my hypotheses. Habitat generalists that had smaller body sizes and smaller home ranges (such as the raccoon and opossum) showed positive relationships to increased human activities and disturbances. The probability of raccoon site use decreased substantially after natural land cover exceeded approximately 90%. Increased use and occurrence by raccoons near human-modified landscapes is consistent with the findings of Prange and Gehrt (2004), Randa and Yunger (2006), Markovchick-Nicholls et al. (2008), and Ordeñana et al. (2010). Sixteen sites (22%) had a probability of use equal to or near one. These sites had the lowest standard errors with some converging on zero. Among all sites (used or not) the lowest proportion of natural land cover was 0.64 and 56 (78%) of the sites had natural land cover greater than 90%.

The limited range of data for this covariate brings into question how raccoon resource use would change in sites with extremely low proportions of natural land cover (e.g., highly urbanized areas). If raccoons show affinity to urban edge (Ordeñana et al. 2010) but still require vegetative cover such as that provided by greenspaces and natural landscaping (Bateman and Fleming 2012) then it can be assumed that sites containing very high proportions of impermeable surface may deter use by raccoons (and possibly other carnivore species). This may indicate the proportion of natural land cover and the probability of raccoon occurrence would have a parabolic relationship and the probability of occurrence would equal zero below some minimum threshold of

natural land cover. Besides their generalist niche, raccoons are exceedingly adept in the exploitation of anthropogenic resources through advantageous features such as excellent dexterity, intelligence, and high fecundity (Gehrt et al. 2010).

Randomly selected sites within the west Austin region were restricted to those that exceeded 100 m from the nearest urban edge. Without this limitation, there may have been a greater opportunity to sample sites with greater proportions of non-natural land cover, thus, a wider range of covariate values and fewer sites with natural cover in excess of 90%. Another way to increase variation in land cover covariates could have been the use of site stratification to ensure sufficient sampling of both urban and rural sites. Even though detection probability was low for the raccoon ($p = 0.11$, $SE = 0.02$), naïve use (0.22) was very similar to the proportion of sites used by raccoons (0.25) in the Markovchick-Nicholls et al. (2008) study.

The probability of opossum site use was positively influenced by the availability of urban and altered land and negatively influenced by the proportion of natural cover. Although competitive ($\Delta AIC_c < 2$), the covariates of these models are highly correlated leaving some uncertainty as to which models provide the best description of site use. However, all three models represent a positive response to human-altered landscapes. This is consistent with the findings of Markovchick-Nicholls (2008) and Crooks (2002) but inconsistent with Ordeñana et al. (2010) who found no significant correlations between opossum occurrence and urban proximity. Prange and Gehrt (2010) also found Virginia opossums to occur more frequently in rural areas than urban when compared to raccoons. In southern California, opossums reached higher relative abundances and had

higher track frequencies in smaller habitat patches which could lead to increased probability of detection in those areas (Crooks 2002).

In my study, there were a total of 16 sites (22%) that were within 400 meters of urban land cover. All of these “urban” sites were found within study areas that had relatively high levels of surrounding urbanization; i.e., > 15% urban land within 3 km. Also, 81% of these urban sites were found in the three smallest study areas. Therefore, if opossums in central Texas are concentrated in small natural areas surrounded by urbanization, then the probability of use will be higher than in larger natural areas where density is lower (e.g., BCNWR). However, in low density sites more survey effort may be needed to get better estimates of use.

Results for grey fox were as expected with equal probability of use across all sites. The null models had the greatest weight ($w_i = 0.17$) and indicated that there was a 72% chance that the species would use any site at random. Though the grey fox is considered to be a generalist species and has been observed to utilize habitat near urban areas (Harrison 1997; Crooks 2002; Riley 2006), Ordeñana et al. (2010) found grey fox occurrence to be negatively related to percent urban land cover within 3 km of a camera station and Markovchick-Nicholls et al. (2008) found grey foxes to be negatively associated with road intensity indicating some negative effect of anthropogenic activities and infrastructure on fox habitat use. Harrison (1997) found that grey foxes may benefit from access to urban habitats although they avoided residential areas when population densities exceeded 50 residents/km². This behavior may not have been revealed in my study because only a few sites had a high proportion of urban land cover.

Further, I did not take into consideration human population densities. Also, the most-supported models (nearrd, neartrl, and alt; all with $0.10 < w_i < 0.15$) had covariate coefficient estimates with large standard errors thus indicating uncertainty in the covariate's influence. Because models in the set were so closely competing more research should be done to investigate possible urban influence on fox occurrence before ruling out such relationships. Coyote site use was strongly and positively influenced by urban intensity within 3 km of study area. Therefore, coyotes are more likely to use sites within smaller study areas that have a high degree of surrounding urbanization than large areas with little surrounding urban land cover. Coyotes have commonly been observed using developed areas and may travel between habitat fragments and cross roads (Tigas et al. 2002; Gehrt et al. 2009; Gehrt et al. 2010). Moreover, coyotes residing in areas with higher proportions of non-natural habitat have been noted to maintain either larger or smaller home ranges depending on resource availability (Bateman and Fleming 2012). However, evidence suggests that coyotes may be more likely to inhabit more rural areas (Randa and Yunker 2006) and most likely require abundant natural cover (Atwood 2006) or connected patches of natural habitat (Tigas et al. 2002) to sustain populations.

All of my more developed study regions contained multiple parks and/or greenspaces, often connected by riparian corridor that could facilitate movement through an urban matrix. In addition, water availability may have been a limiting factor for coyotes at Balcones Canyonlands NWR which would account for a fair proportion (48%) of unused sites. Conversely, Pedernales Falls State Park is transected by the

Pedernales River but did not contribute any detections. However, the park did account for an additional 30% of the unused sites. In spite of the possibility of urban coyotes maintaining larger home ranges, they have also been noted to display more pack-like behavior (Bateman and Fleming 2012) that could increase population density and detection probabilities in those areas. Coyote density may also be higher in urban areas if they suffer constricted home ranges, possibly due to restricted movement if the landscape is severely fragmented.

Very little information is available regarding the effects of urban development on ringtail occurrence. Ringtails are considered generalist omnivores (Schmidly 1994; Harrison 2012) that utilize anthropogenic resources for cover (Castellanos and List 2005) as well as roads and trails (Barja and List 2006). All models in the set had some support ($\Delta AIC_c < 3$) in describing ringtail occurrence which indicates urbanization may influence site use but was not adequately captured by the presence-absence data or choice of covariates. Therefore, the null model was favored and ringtail occurrence was estimated to be equal across all study sites with nearly a 50% chance of any site being used. This would suggest that even though ringtails are known for being cryptic, they are not uncommon across our study areas. Low ringtail trap success by Harrison (2012) indicates that ringtail probability of detection may also be very low leading to unreliable estimates of ψ and associated covariate coefficients.

Cottontail site use was negatively influenced by the total amount of available habitat area. Hunt et al. (2014) found smaller home range size and higher survival for eastern cottontails in more developed sites in urban Chicago. These rabbits were also

observed in much higher densities than previously reported by other studies. Like several of the other mammal species that have potential to sustain higher densities in urban areas, detection probabilities may be higher at these sites leading to unaccounted-for heterogeneity in p . Since cottontail and coyote site use appears to share similarities (greatest site use in smaller areas and less in larger) we have no reason to believe coyote presence has a negative effect on cottontail persistence from a predator-prey standpoint, at least for my study areas in central Texas. In addition, Morey et al. (2007) found the diets of coyotes in metropolitan Chicago to be more diverse than the diets of more rural coyotes. This could decrease predation rates and might explain higher rates of use or higher densities for urban cottontails. It is also important to note that the scent lures (used in the present study) are formulated to attract carnivorous species and may not serve as an accurate method in assessing population parameters of cottontails or other non-predator species. As such, detection probability and site use may have been underestimated for cottontails.

Assessment of detection probabilities

Estimates of site occupancy or use may be unreliable when detection probability is low (< 0.15) and survey effort is insufficient (< 7 occasions), especially when estimates of ψ approach 1 (MacKenzie et al. 2002). Many of my site estimates of ψ that approach 1 should be interpreted with caution, especially for those species with very low detection probabilities. Species with low detection probabilities have an increased bias in the proportion of sites they are detected in at least once (MacKenzie and Bailey

2004). False absences may arise when the probability of detecting a species is very low and enough surveys have not been conducted to ensure the species will be detected when present. The effect of false absences can be best demonstrated for those species whose averaged estimates of probability of use ($\bar{\psi}$) are much larger than the naïve estimate of ψ (MacKenzie et al. 2002) (Table 10), indicating uncertainty in detecting the species when present. Generally, species that had probabilities of detection less than 0.1 (skunk and coyote) did not produce reliable estimates of use unless naïve estimates were greater than 0.2 (e.g., ringtail) or covariates were included that accounted for heterogeneity in site use. This improved site use estimates 1.5 times or greater than the naïve estimates (e.g., opossum and cottontail). Species that had detection probabilities greater than 0.1 and naïve estimates of site use greater than 0.3 (e.g., raccoon and grey fox) produced models of estimated site use less than 1.3 times that of naïve estimates.

Since species like the ringtail, striped skunk, and opossum require survey periods of approximately 49, 72, and 31 occasions respectively to be $\geq 95\%$ sure the species is detected when present, uncertainty exists with only 14 sampling occasions. After 14 days, I am only 58%, 44%, and 73% certain of detecting the ringtail, striped skunk, and opossum, respectively, when present. However, I am 94% certain to detect a grey fox when present during the same sampling period (Figure 6).

Increasing the number of sampling occasions and sites can improve both accuracy and precision with the greatest improvements realized in species with very low detection probabilities (MacKenzie et al. 2002). If a species is present but went undetected, then relationships between covariate data and the probability of site use

may be overlooked or misrepresented. Inferences of parameter estimates are most robust when the probability of a false absence $[(1-p)^k]$ is between 0.05 - 0.15 (MacKenzie et al. 2006). Higher probabilities may indicate that not enough survey effort is being expended to ensure detection of the species. Detectability of the opossum, raccoon, and coyote follow similar patterns to the estimates of latency to initial detection (LTD) presented by Gompfer et al. (2006) who found coyotes to be the most wary species with a similar LTD (approximately 40 days) to opossums, both of which took longer to detect than the raccoon. Gompfer et al. (2006) also found that besides the coyote, smaller-bodied mammal species like the marten and weasel, that are similar in size to the ringtail, had lower detectability. Furthermore, ringtails and opossums are typically solitary (Schmidly 1994) which could be an indication of lower population densities, territorial behavior, or lower probability of being detected during any sampling occasion. Only the raccoon and grey fox, who are reportedly more social (Schmidly 1994; Gehrt et al. 2010), were sometimes photographed with more than one individual in the field of view. Without sufficient survey effort to ensure detection of a species when present, uncertainty in accounting for false absences leads to poor estimates of ψ .

Large mammals, such as the coyote and grey fox, cover more extensive home ranges than most smaller mesocarnivores (Gehring and Swihart 2003) thus the “size” of a site (i.e., spacing between adjacent sites) must take into account the behavior of that animal accordingly in order to make accurate inferences about site use (MacKenzie et al. 2006). In order to meet these standards, sites for larger species were restricted to

camera stations at least 1 - 1.5 km apart which reduced the overall sample size for those species. Since the precision of an estimator increases with sample size and bias increases with low detection probabilities (MacKenzie et al. 2006) we would expect parameter estimates to be less reliable for our large mammal models, especially with a low probability of detecting a species after fourteen surveys.

In order to make useful inferences about ψ in a logistically feasible time-frame, more effective methods could be used to increase the probability of detection for each species. Such methods could include additional game cameras at each station, using multiple camera stations at each site, and incorporating additional survey techniques, such as track plates or collecting scat, to increase the probability of detecting a species at a site when present.

Heterogeneity in detection probability can arise from environmental factors, seasonal behavior, and relative abundance and if not accounted for, may result in negatively biased occupancy estimates (MacKenzie et al. 2006). Sites at which species abundance is higher would also have a greater probability of detecting that species during any single sampling occasion unless populations at all locations are relatively large (Mackenzie et al. 2006). Detection probabilities that vary according to site-specific relative abundance can be estimated as:

$$p(N_i, r) = 1 - (1 - r)^{N_i}$$

where p is a function of N_i (the abundance at site i) and r (the individual detection probability). If considerable variation in abundance exists among sites then occupancy modeling may not be the most appropriate approach for describing the population state

(Mackenzie et al. 2006). Presence/absence data can be used to estimate abundance (Royle and Nichols 2003) but this is beyond the scope and design of the present study.

Assessment of model fit

Occupancy models for the grey fox showed overdispersion with $\hat{c} \gg 1$. Model overdispersion may be the result of non-independent detection histories. This is usually the case when sites are not spaced far enough apart and animals can move among sites during the survey period (MacKenzie and Bailey 2004). Non-independence between sites may also lead to more sites being occupied than the actual local population size for that species resulting in overestimates of occupancy (and abundance) and underestimated standard errors (MacKenzie et al. 2004). I do not feel this is the case in my study since distance between sites was based on normal home range sizes for each species and study areas were large enough to support populations greater than the number of sites used in the given area.

A closer look at raw detection data also fails to show evidence of a single species or individual appearing at two or more adjacent camera stations during the same sampling occasion. I feel that poor model fit for the grey fox was probably the result of a few unexpected detection histories. For example, one of the observed detection histories ($h_{29} = [11011101001001]$) had an expected value of only 6×10^{-7} and thus it alone contributed to > 97% of the χ^2 test statistic. The grey fox was the only species that had more variation in the observed data than expected ($\hat{c} > 1$), except for the opossum model 'nat' which had \hat{c} values larger than one but only border-line significant ($p =$

0.054). All other species had less ($\hat{c} < 1$) indicating possible bias in the models. However, even with potential bias in estimating ψ , logistic regression still has the ability to capture relationships between covariates and the probability of site use.

Management implications

Because raccoons, opossums, grey foxes, and ringtails have all been observed to act as predators of songbird nests, care must be taken when planning urban preserves and greenspaces, especially in areas with threatened avian species. Nest success may be compromised in highly urbanized areas that are designated as protected habitat (e.g., federally-endangered Golden-cheeked warbler) such as those in the San Marcos, San Antonio, and west Austin study regions. There is little evidence from my findings to suggest that recreational trail density or proximity to a trail increases use by raccoons or opossums but I lack evidence to dismiss any effect trails may have on ringtail or grey fox habitat use. Miller and Hobbs (2000) found that mammalian nest predators avoided nests near trails so the concerns expressed by Sinclair et al. (2005) over increased mammalian nest predation due to the presence of recreational trails may be overstated. However, the magnitude of nest predation by mammals in parks and greenspaces warrants further investigation. In particular, more research is needed addressing the role of ringtails as nest predators, their population dynamics across a gradient of landscapes, and the factors that influence those dynamics. Substantial research has examined the influence of urbanization on coyotes, raccoons, and foxes but very little information exists regarding these species in central Texas, one of the fastest urbanizing

areas in the country. Learning how wildlife responding to urban environments over time can help mitigate or reduce negative human-wildlife interactions and decrease the probability of creating unwanted population sources or sinks.

Conclusion

Mesocarnivore species in central Texas seem to display similar responses to urbanization as do their conspecifics in other regions. Raccoon and opossum habitat use is greater in areas of increased human disturbance than in more rural and isolated sites. This is most likely attributed to the anthropogenic food sources that are provided by human refuse, gardens, pet food, and other sources. There is insufficient evidence to infer positive or negative responses of grey foxes or ringtails to urbanization. This may be due to unmodeled heterogeneity in detection and/or occurrence or perhaps these species are in fact urban neutral. Results suggest that cottontails prefer smaller areas of natural habitat although they may also be urban neutral. Based on my data, I am confident that the covariates selected for each species accurately describe factors that influence species site use. However, low detection probabilities suggest the possibility that false absences existed for all of the reported species, excluding the grey fox. In general, false absences can sometimes bias estimates of ψ and associated covariates. Greater variation in covariate data, increasing the probability of detecting a species when present, and a larger sample size could ensure stronger insight into how urbanization influences spatial distribution and habitat use by mesocarnivores.

Table 1. Correlations at 400 m

Correlation table for all ψ covariates. Site-level covariates calculated for the 400 m buffer.

400 M CORR.	rds	trls	nat	alt	Urb	area	nearhab	Neartrl	nearrd	3km
rds	1.00									
trls	0.35	1.00								
nat	-0.66	-0.42	1.00							
alt	0.55	0.48	-0.73	1.00						
urb	0.60	0.40	-0.75	0.69	1.00					
area	-0.35	-0.14	0.40	-0.45	-0.37	1.00				
nearhab	-0.28	-0.37	0.41	-0.43	-0.32	0.44	1.00			
neartrl	-0.05	-0.27	0.19	-0.17	-0.09	0.26	0.30	1.00		
nearrd	-0.39	-0.45	0.44	-0.49	-0.39	0.49	0.79	0.33	1.00	
3km	0.50	0.33	-0.61	0.70	0.57	-0.61	-0.35	0.03	-0.39	1.00

Table 2. Correlations at 800 m

Correlation table for all ψ covariates. Site-level covariates calculated for the 800 m buffer.

800 M CORR.	rds	trls	nat	alt	urb	area	nearhab	Neartrl	nearrd	3km
rds	1.00									
trls	0.27	1.00								
nat	-0.89	-0.24	1.00							
alt	0.57	0.21	-0.58	1.00						
urb	0.68	-0.04	-0.72	0.72	1.00					
area	-0.47	0.09	0.49	-0.44	-0.59	1.00				
nearhab	-0.67	-0.35	0.55	-0.69	-0.57	0.51	1.00			
neartrl	-0.26	-0.22	0.37	-0.21	-0.09	0.26	0.32	1.00		
nearrd	-0.65	-0.35	0.51	-0.58	-0.51	0.49	0.80	0.29	1.00	
3km	0.59	0.08	-0.71	0.68	0.83	-0.61	-0.52	-0.25	-0.43	1.00

Table 3. Raccoon model ranking

Model set of covariates influencing probability of use for the northern raccoon. Models ranked by AIC_c score and ordered by descending weights.

MODEL	ΔAIC_c	w_i	(-2LL)
psi(nat),p(.)	0.00	0.994	361.85
psi(rds),p(.)	12.57	0.002	374.42
psi(urb),p(.)	12.94	0.002	374.79
psi(alt),p(.)	13.06	0.001	374.91
psi(3km),p(.)	15.05	0.001	376.90
psi(trls),p(.)	18.79	< 0.001	380.64
psi(nearhab),p(.)	18.85	< 0.001	380.70
psi(neartrl),p(.)	19.21	< 0.001	381.06
psi(.),p(.)	19.55	< 0.001	383.58
psi(area),p(.)	19.98	< 0.001	381.83

Table 4: Opossum model ranking

Model set of covariates influencing probability of use for the opossum. Models ranked by AIC_c score and ordered by descending weights.

MODEL	ΔAIC_c	w_i	(-2LL)
psi(urb),p(.)	0.00	0.334	186.88
psi(nat),p(.)	0.21	0.301	187.09
psi(alt),p(.)	1.49	0.159	188.37
psi(rds),p(.)	3.40	0.061	190.28
psi(3km),p(.)	4.01	0.045	190.89
psi(nearrd),p(.)	4.57	0.034	191.45
psi(area),p(.)	5.97	0.017	192.85
psi(.),p(.)	6.03	0.016	195.09
psi(nearhab),p(.)	6.45	0.013	193.33
psi(neartrl),p(.)	6.76	0.011	193.64

Table 5: Coyote model ranking

Model set of covariates influencing probability of use for the coyote. Models ranked by AIC_c score and ordered by descending weights.

MODEL	ΔAIC_c	w_i	(-2LL)
psi(3km),p(.)	0.00	0.966	143.98
psi(urb),p(.)	7.60	0.022	151.58
psi(area),p(.)	10.22	0.006	154.20
psi(alt),p(.)	11.38	0.003	155.36
psi(nat),p(.)	12.62	0.002	156.60
psi(rds),p(.)	15.52	< 0.001	159.50
psi(neartrl),p(.)	16.21	< 0.001	160.19
psi(nearhab),p(.)	16.21	< 0.001	160.19
psi(.),p(.)	16.02	< 0.001	162.36
psi(nearrd),p(.)	17.32	< 0.001	161.30

Table 6: Ringtail model ranking

Model set of covariates influencing probability of use for the ringtail. Models ranked by AIC_c score and ordered by descending weights.

MODEL	ΔAIC_c	w_i	(-2LL)
psi(.),p(.)	0.00	0.171	214.91
psi(alt),p(.)	0.69	0.121	213.40
psi(area),p(.)	0.87	0.110	213.58
psi(urb),p(.)	0.88	0.110	213.59
psi(nearrd),p(.)	1.15	0.096	213.86
psi(neartrl),p(.)	1.37	0.086	214.08
psi(nat),p(.)	1.85	0.068	214.56
psi(nearhab),p(.)	1.94	0.065	214.65
psi(trls),p(.)	2.13	0.059	214.84
psi(3km),p(.)	2.15	0.058	214.86

Table 7: Grey fox model ranking

Model set of covariates influencing probability of use for the grey fox. Models ranked by AIC_c score and ordered by descending weights.

MODEL	ΔAIC_c	w_i	(-2LL)
psi(.),p(.)	0.00	0.171	464.88
psi(nearrd),p(.)	0.32	0.146	462.93
psi(neartrl),p(.)	0.54	0.131	463.15
psi(alt),p(.)	0.98	0.105	463.59
psi(area),p(.)	1.72	0.072	464.33
psi(nearhab),p(.)	1.78	0.070	464.39
psi(nat),p(.)	1.89	0.067	464.50
psi(urb),p(.)	1.93	0.065	464.54
psi(rds),p(.)	2.08	0.061	464.69
psi(3km),p(.)	2.21	0.057	464.82

Table 8. Cottontail model ranking

Model set of covariates influencing the probability of site use by the eastern cottontail rabbit. Models ranked by AIC_c score and ordered by descending weights.

MODEL	ΔAIC_c	w_i	(-2LL)
psi(area),p(.)	0.00	0.393	178.50
psi(trls),p(.)	2.00	0.145	180.50
psi(3km),p(.)	2.78	0.098	181.28
psi(.),p(.)	2.90	0.092	183.58
psi(nearrd),p(.)	3.97	0.054	182.47
psi(urb),p(.)	4.49	0.042	182.99
psi(rds),p(.)	4.57	0.040	183.07
psi(alt),p(.)	4.66	0.038	183.16
psi(nat),p(.)	4.86	0.035	183.36
psi(neartrl),p(.)	5.00	0.032	183.50

Table 9. Species urban scores

Urban scores suggesting positive (>0) or negative (<0) effects of urbanization on each species. Values correspond to partial covariate coefficients before being adjusted by model weight and the y-intercept of ψ for the null model. Coefficient sign for urban influence adjusted by $+1/-1$.

ψ (COV)	Raccoon	Opossum	Ringtail	Skunk	Grey Fox	Coyote	Cottontail
rds	1.00	1.32	-0.07	0.80	-0.15	1.17	0.24
trls	0.59	0.34	-0.11	0.61	-0.04	-0.15	-4.91
nat	-6.27	-3.78	-0.35	-1.19	0.22	-2.05	-0.16
alt	1.84	1.86	1.16	1.51	-0.83	***	0.46
urb	2.47	2.31	1.55	***	-0.44	***	0.62
area	-0.38	-0.60	0.45	-0.72	0.29	-1.80	-1.17
nearhab	-0.48	-0.47	-0.21	-4.39	0.26	***	-0.07
neartrl	-0.48	-0.45	0.34	***	0.58	***	-0.10
nearrd	***	-0.82	0.44	-1.03	0.64	***	-0.42
3km	0.77	0.70	0.12	0.44	-0.09	24.21	0.50
null y-int	-0.14	-1.04	-0.04	***	-0.92	2.91	-0.97
URBAN SCORE	6.25	2.35	0.22	***	-0.20	***	-0.01

*** Model did not reach numerical convergence or had excessive error.

Table 10. Species p and $\bar{\psi}$
Averaged estimates of occurrence and detection probabilities across all sites based on top ranked models for each species. Naïve $\psi = x/s$ and N is the sample size. Estimates of ψ for the opossum were averaged based on model weight.

Species	Model(s)	N	p	Naïve ψ	$\bar{\psi}$	\overline{SE}	\hat{c}
Raccoon	psi(nat),p(.)	72	0.11	0.38	0.49	0.08	0.22
Opossum	psi(urb),p(.)	72	0.09	0.18	0.24	0.07	0.94
	psi(nat),p(.)	-	-	-	-	-	2.50
	psi(alt),p(.)	-	-	-	-	-	0.63
Ringtail	psi(.),p(.)	64	0.06	0.27	0.49	0.15	0.18
Striped Skunk	psi(neartl),p(.)	70	0.04	0.15	***	***	***
Grey Fox	psi(.),p(.)	49	0.17	0.65	0.72	0.08	4.99
Coyote	psi(3km),p(.)	38	0.07	0.32	***	***	***
Cottontail	psi(area),p(.)	72	0.08	0.18	0.28	0.10	0.22

***Model did not reach numerical convergence or had excessive error.

Figure 1: Influence of “nat” on raccoon use
Influence of proportion of natural land cover within 400 m on the probability of site use by raccoons.

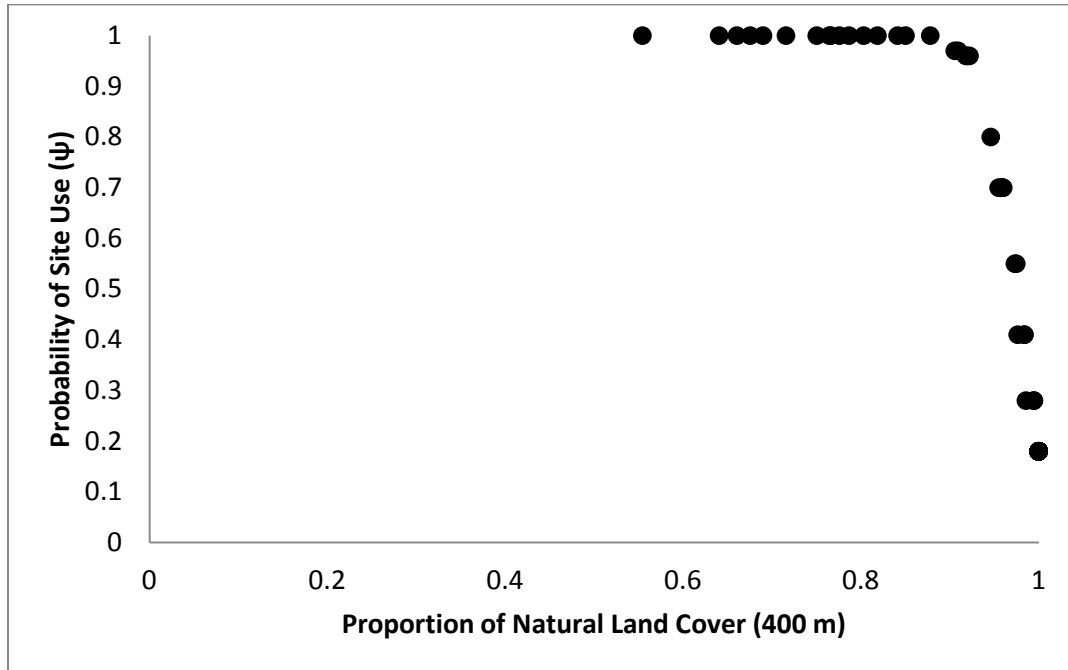


Figure 2: Influence of “nat” on opossum use
Influence of proportion of natural land cover within 400 m on the probability of site use by opossums.

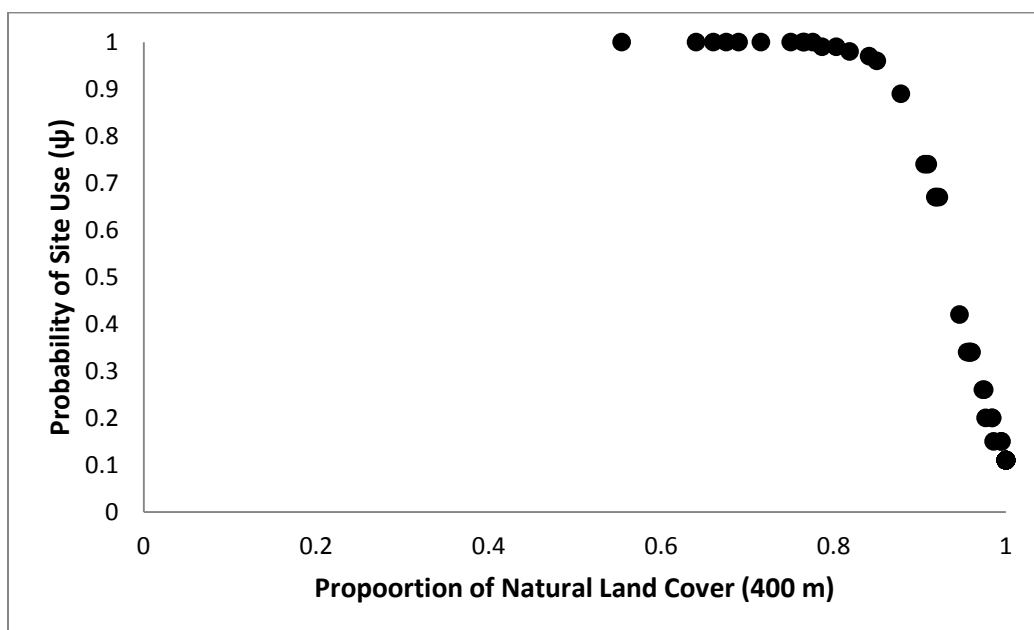


Figure 3: Influence of “urb” and “alt” on opossum use
 Influence of presence of urban (Urb) and altered (Alt) land cover within 400 m on the probability of site use by opossums. Magnitude of influence for each covariate and estimates of ψ assessed independently. Bars represent SE.

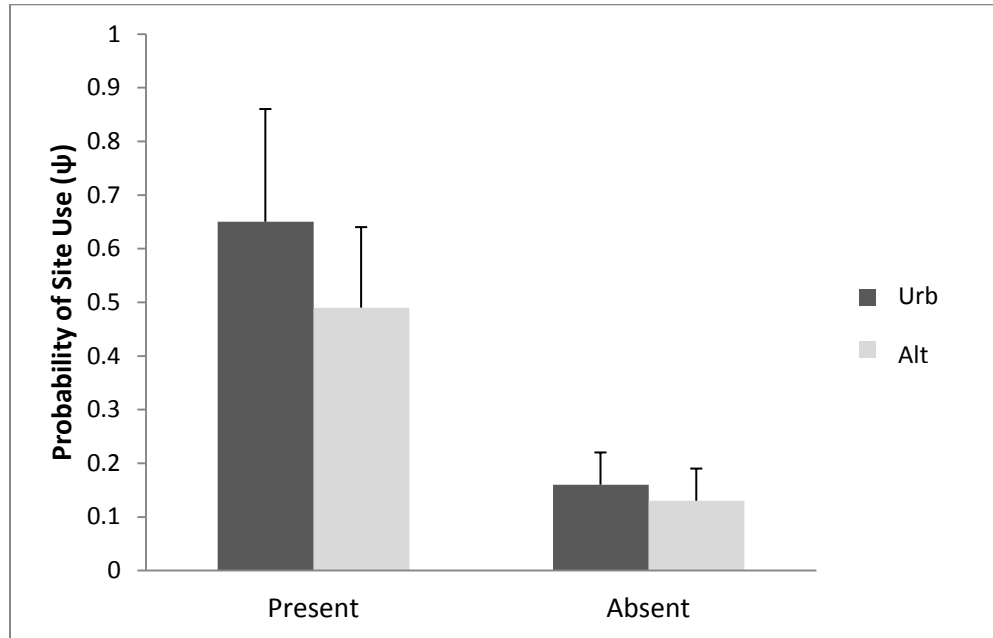


Figure 4: Influence of “area” on cottontail use
 Influence of usable habitat area of study area on the probability of area use by eastern cottontail rabbits. Bars represent \overline{SE} .

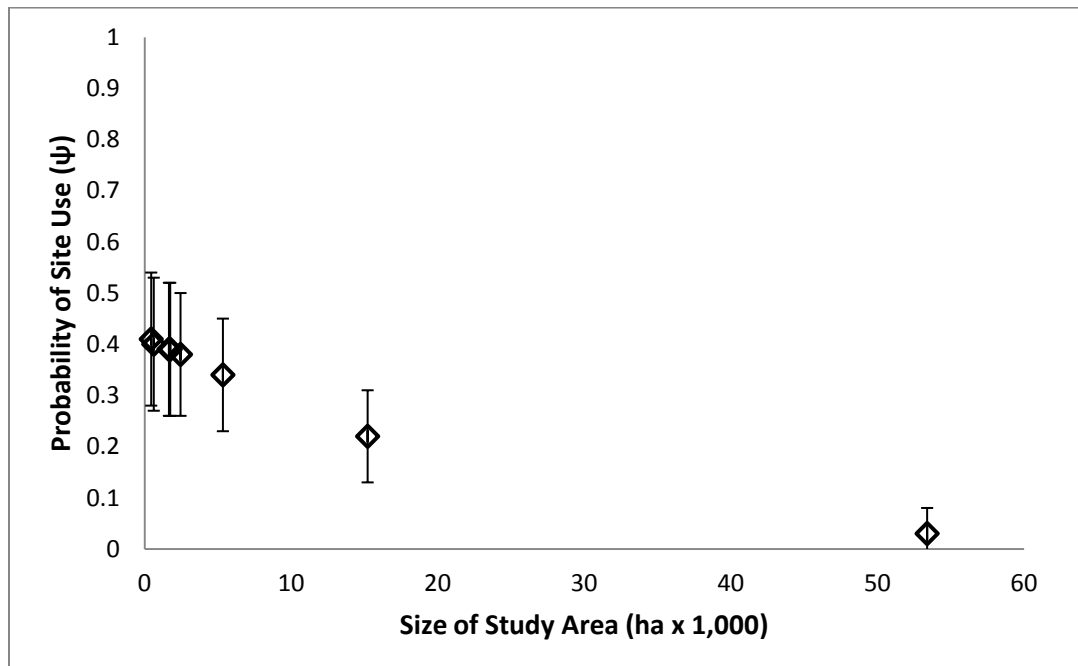


Figure 5: Average occurrence across study regions

Averaged probability of occurrence for the raccoon, opossum, ringtail, fox, and cottontail within each of the major study regions. Bars represent \overline{SE} . The ringtail was excluded from McKinney Falls (MF). See Appendix A for study region details.

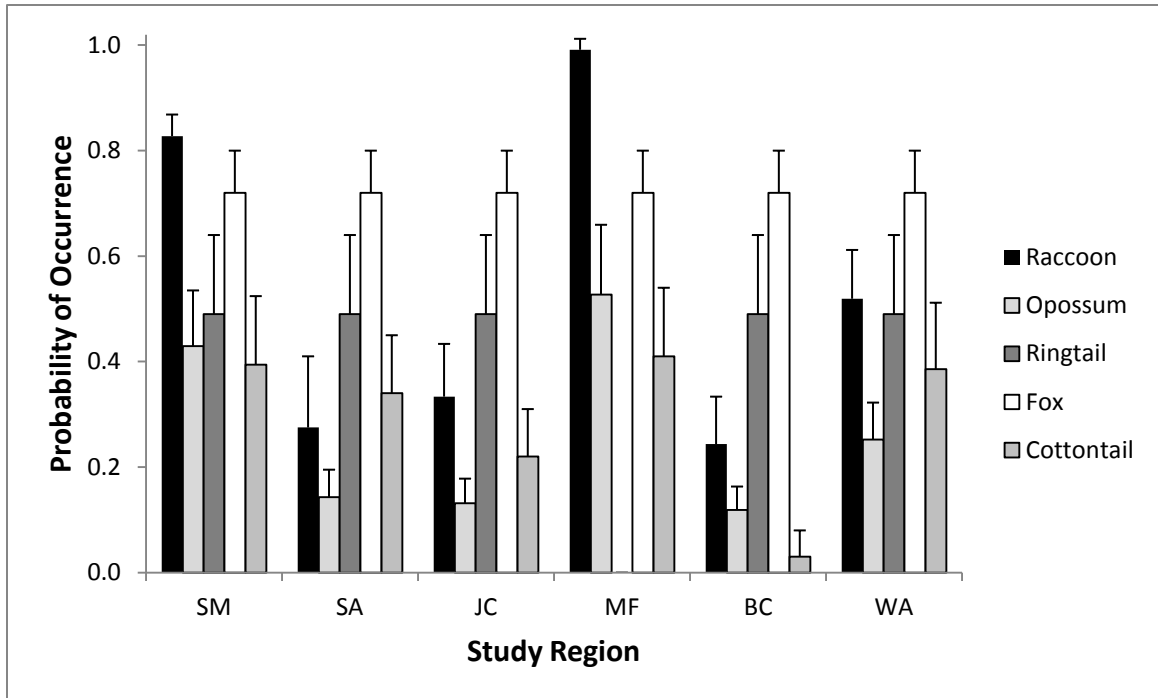
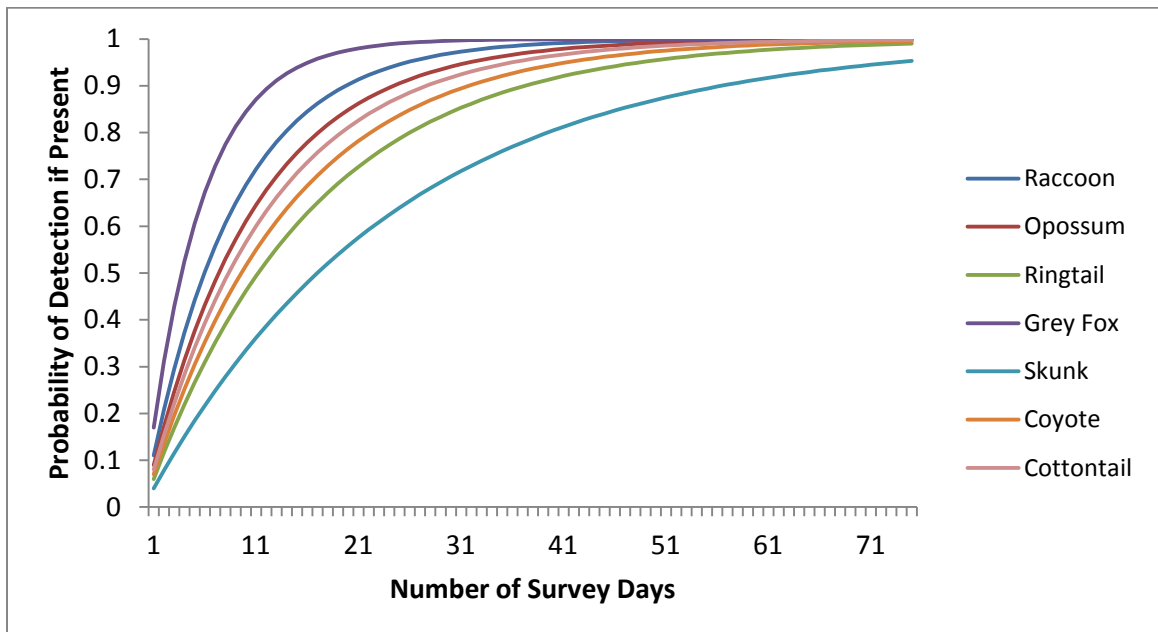


Figure 6: Number of surveys needed for detection

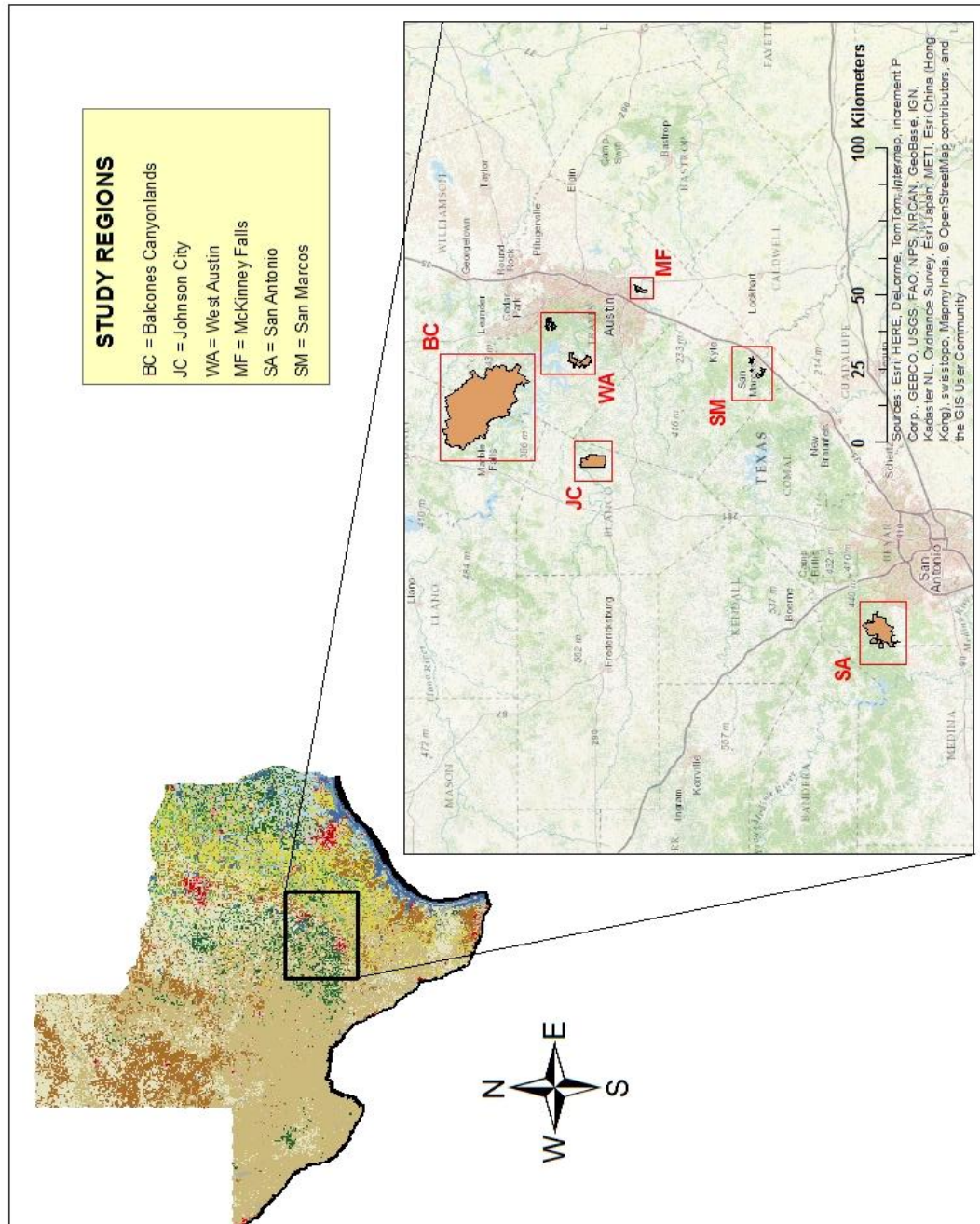
The number of survey occasions needed to detect raccoon, opossum, ringtail, grey fox, skunk, coyote, and cottontail with 95% certainty.



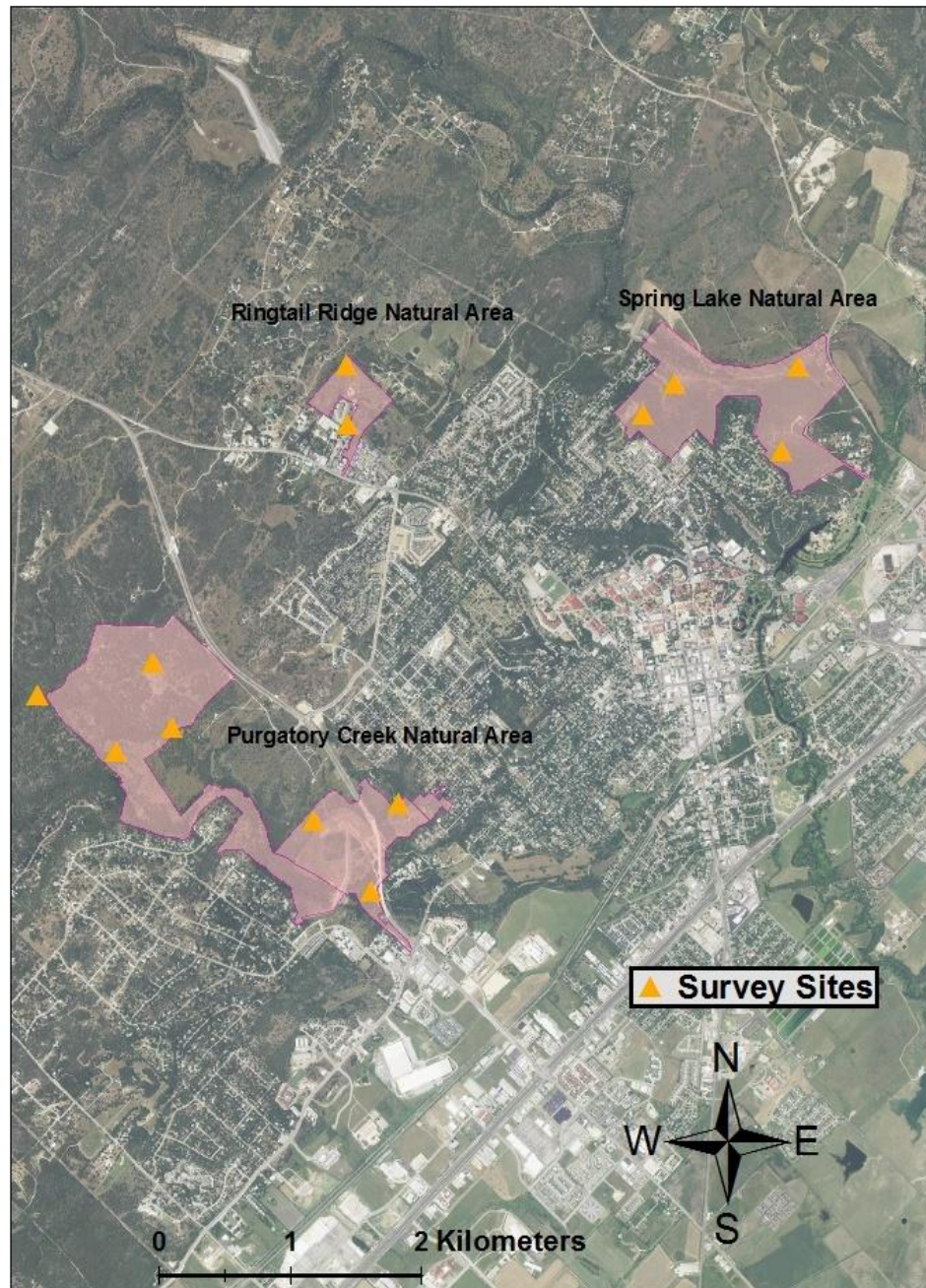
APPENDIX SECTION

APPENDIX A

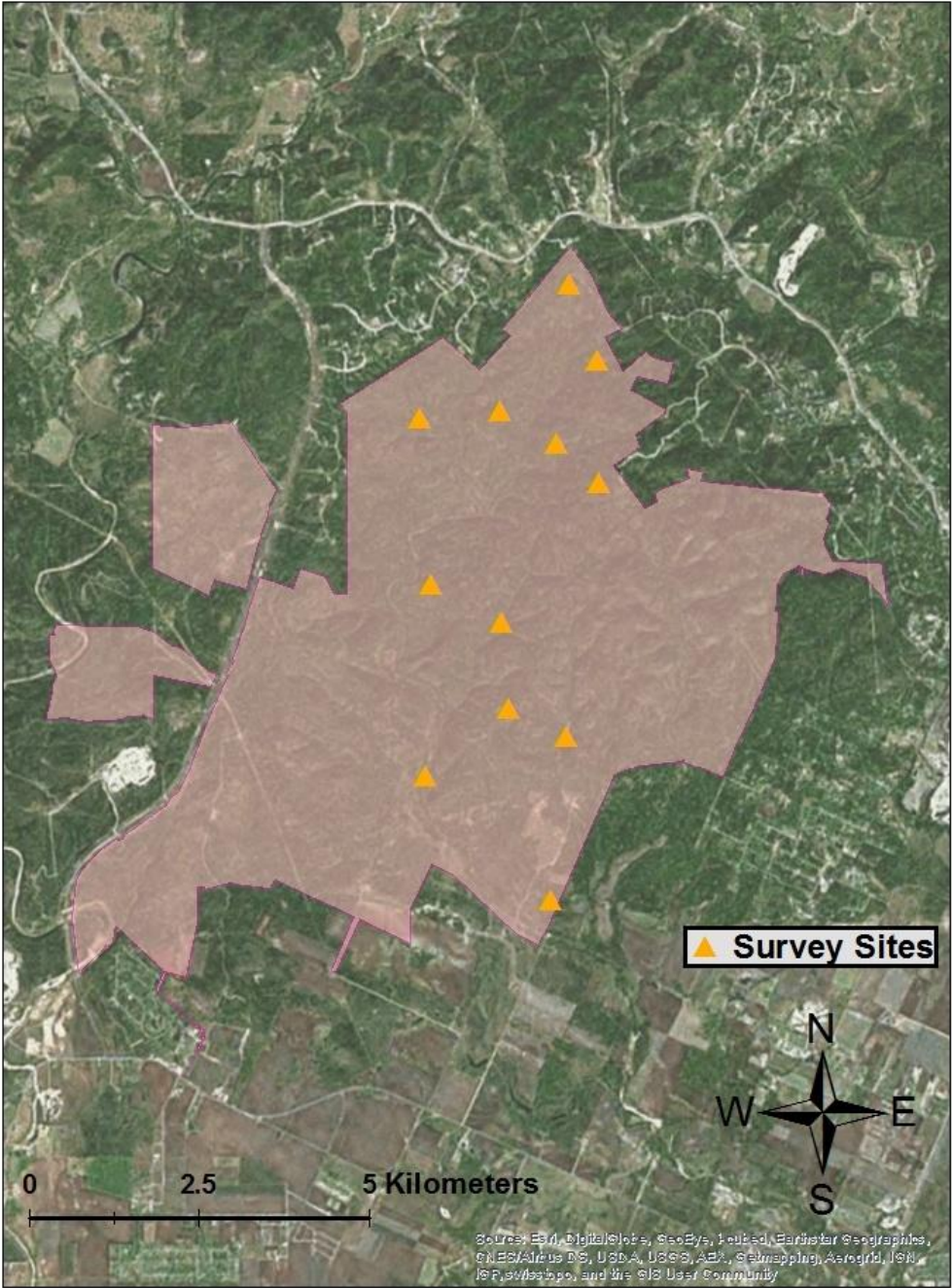
Map A1. All six study regions located within approximately 50 km of the I-35 corridor along eastern Edwards Plateau. Map of Texas displayed as NLCD 2006 land cover classes with red denoting areas of high urban intensity.



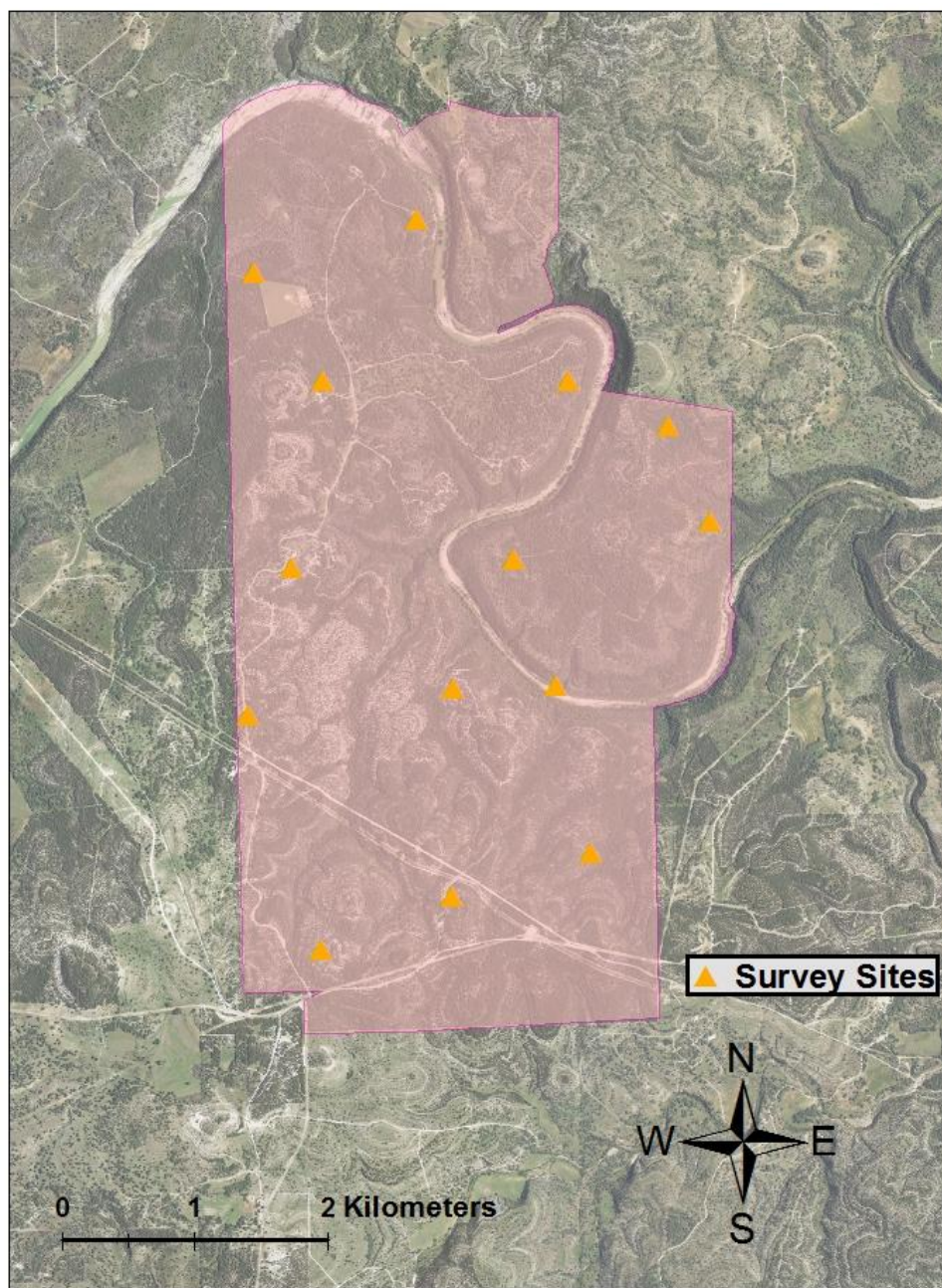
Map A2. San Marcos study region with the Purgatory Creek Natural Area, Spring Lake Natural Area, and Ringtail Ridge Natural Area study areas.



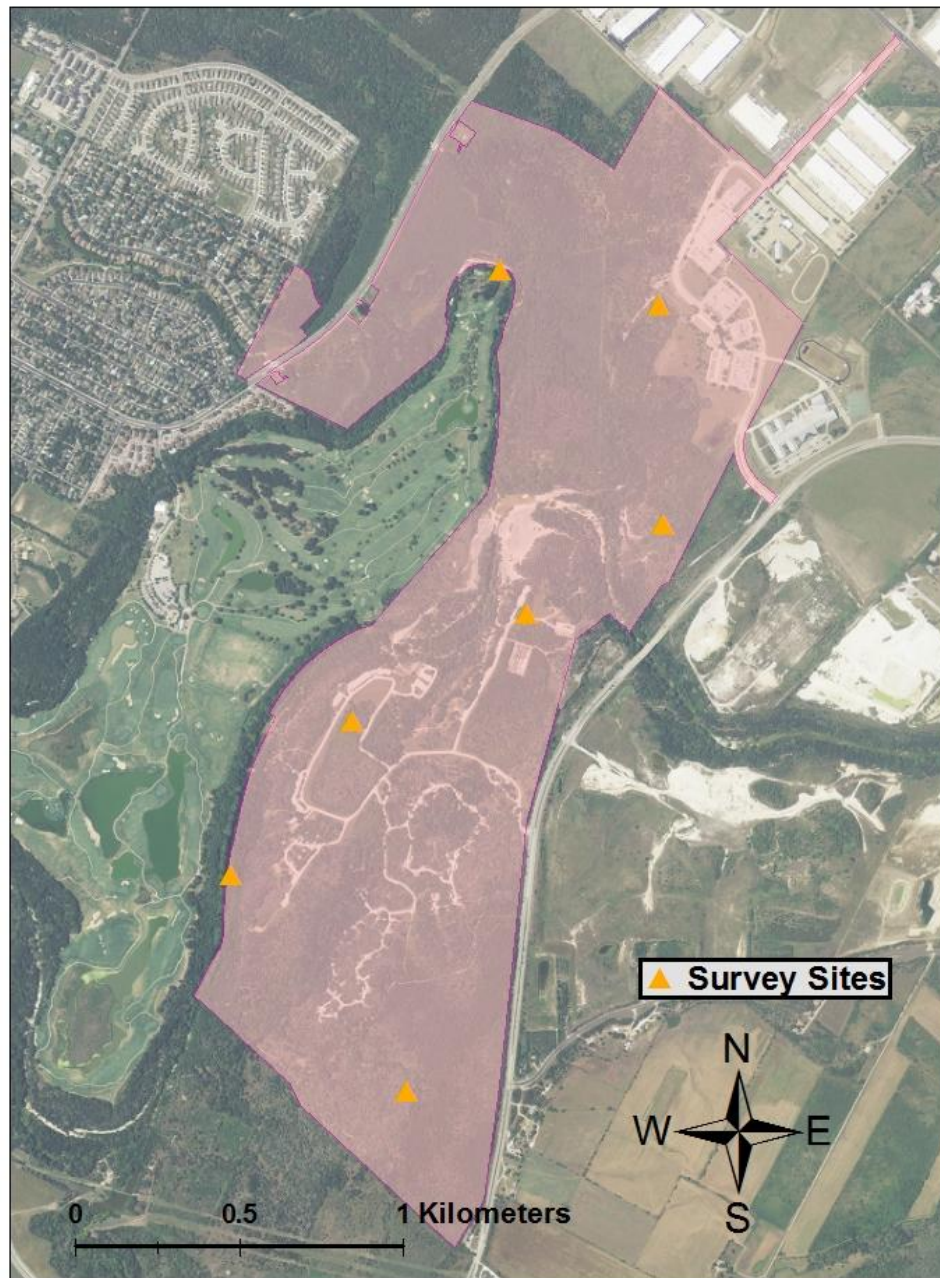
Map A3. San Antonio study region with the Government Canyon State Natural Area study area.



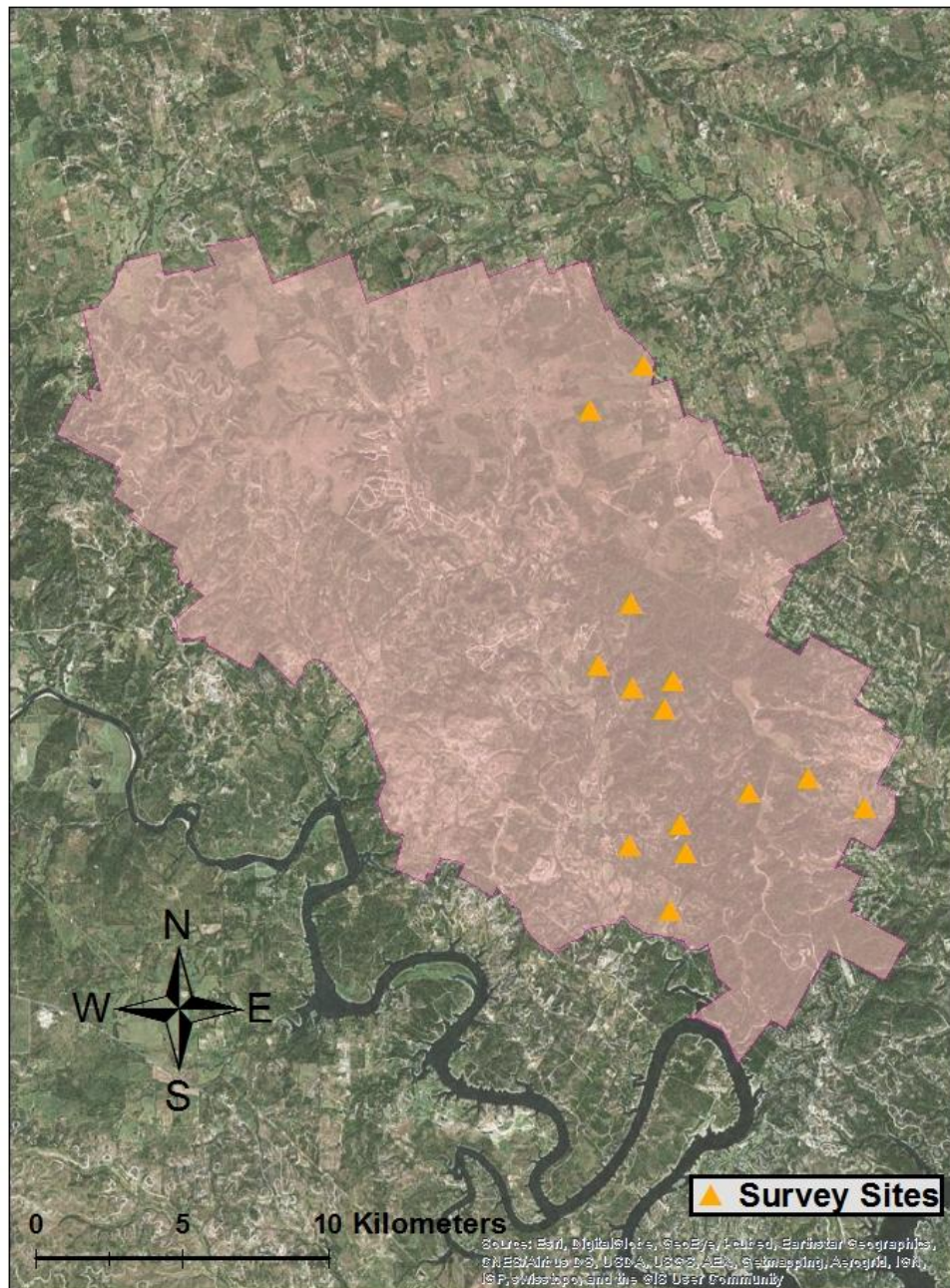
Map A4. Johnson City study region with the Pedernales Falls State Park study area.



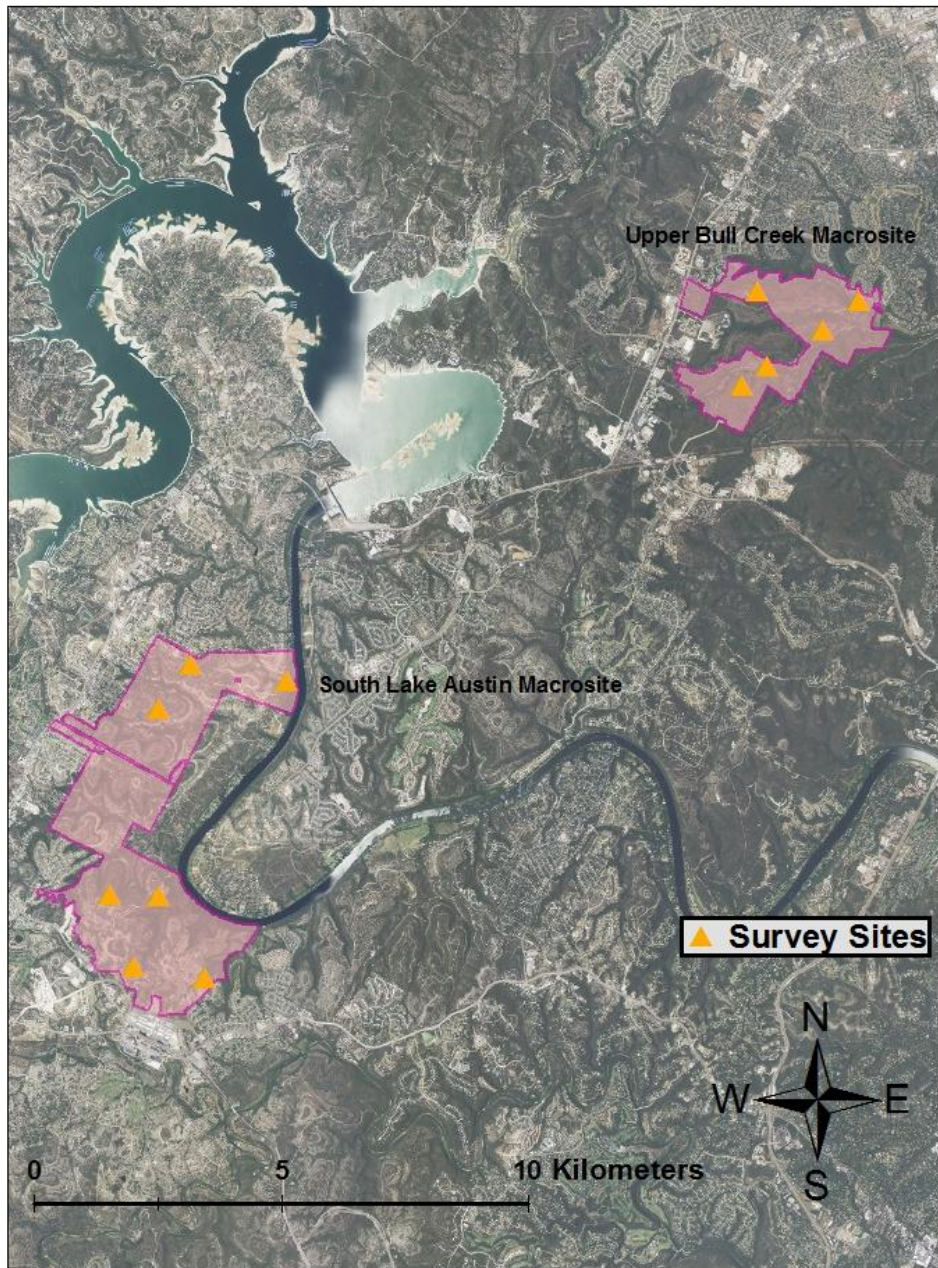
Map A5. McKinney Falls study region with the McKinney Falls State Park study area.



Map A6. Balcones Canyonlands study region with the Balcones Canyonlands National Wildlife Refuge study area.



Map A7. West Austin study region with the Upper Bull Creek Macrosite and South Lake Austin Macrosite study areas



APPENDIX B

Purgatory Creek Natural Area

Purgatory Creek (PCNA) is a 230.7 ha city owned, non-profit operated natural area located within the Edwards Aquifer recharge zone. The park lies within the western boundary of the City of San Marcos and follows a portion of Purgatory Creek that runs northwest to southeast. Ranchland, woodlands, prairies and residential neighborhoods surround the natural area. Landscape cover within the park consists of upland meadows, juniper thickets, champion oaks, and a flood control dam and several areas within the park are considered breeding habitat for the GCWA and BCVI. The park offers approximately 14.3 km of single and double track trail for foot or bicycle traffic and leashed pets. In 2011, 43.3 ha adjacent to the northern section of Purgatory Creek Natural area were purchased as an addition to the park and funding for another 37.5 ha, congruent with the newly purchased parcel, has recently been approved.

(www.smgreenbelt.org)

Ringtail Ridge Natural Area

Ringtail Ridge (RRNA) is a 16.2 ha city owned, non-profit operated natural area that lies within the northwestern boundary of the City of San Marcos and was once ranchland and the site of a slaughter plant. Ranchland, residential property and commercial development surround the natural area and landscape cover within the park consists of meadows, oak groves, persimmon thickets and cactus stands. The park

has approximately 4 km of trail available for foot or bicycle traffic and leashed pets, including a 0.8 km handicap accessible crushed gravel path. (www.smgreenbelt.org)

Spring Lake Preserve

Within the north-central city limits of San Marcos, at the headwaters of the San Marcos River, lies Spring Lake Preserve (SLP). The 101.6 ha city owned, non-profit operated park sits half in the Edwards Aquifer recharge zone and entirely in the Sink Creek watershed. Landscape cover within the park consists of sparse meadows and oak-juniper woodlands and is surrounded primarily by ranchland and residential neighborhoods. Spring Lake offers 6.8 km of single and double track trail for foot or bicycle traffic and leashed pets and is considered habitat for the GCWA. (www.smgreenbelt.org)

Government Canyon State Natural Area

Government Canyon (GCSNA) is a 4,684.6 ha state natural area on the northwest outskirts of San Antonio, only approximately 3,500 ha of which are accessible to the public. Topography consists of rugged canyonlands and rolling grasslands and vegetation consists of mostly oak-juniper thickets, characteristic of the Texas Hill Country. The natural area is located in the Leon Creek watershed and Edwards Aquifer recharge zone and is a known breeding site of the GCWA and BCVI. The natural area is divided into a moderately developed frontcountry and a larger less developed backcountry that includes a protected habitat area within the northern portion. A mix of

residential and undeveloped land surrounds Government Canyon. There are over 64 km of mostly single track trails for foot or bicycle traffic and leashed pets are only allowed in the frontcountry. Bicycle traffic is not allowed in the protected habitat area, which is closed to all visitors March through August for GCWA breeding season. Camping has recently been added as a recreational opportunity in the natural area.

(<http://www.tpwd.state.tx.us>)

Pedernales Falls State Park

Pedernales Falls (PFSP) is a 2,109 ha state park located in Johnson City, approximately 96 km west of Austin. The park encompasses several kilometers of the Pedernales River and is surrounded predominately by agricultural land. Landscape within the park ranges from grasslands to oak-juniper woodlands to more heavily wooded areas of pecans, elms and sycamore along the major drainages. The park offers recreational opportunities for camping, fishing, swimming and trail-based activities such as hiking, biking and horseback riding. There are over 48 km of single and double track trail, sixteen of which allow equestrian use. Pedernales Falls State Park is also known breeding habitat for the GCWA. (<http://www.tpwd.state.tx.us>)

McKinney Falls State Park

On the southern outskirts of Austin city limits, at the confluence of Williamson and Onion Creek, lies the 293 ha McKinney Falls State Park (MFSP). McKinney Falls is the only site selected that does not lie immediately within the Edwards Plateau eco-region

but along the border of the plateau and the Blackland Praries. However, due to its close proximity, much of the vegetation and wildlife are similar to that found on the plateau. Surrounding land cover includes commercial and residential developments, two golf courses, farmland and the nearby Austin-Bergstrom International Airport. The park experiences some of the highest visitation rates of any Texas state park and offers recreational opportunities such as camping, swimming, fishing, climbing, hiking, and biking. There are 12.6 km of trail available, 4.5 km of which are paved (<http://www.tpwd.state.tx.us>).

Balcones Canyonlands National Wildlife Refuge

The Balcones Canyonlands National Wildlife Refuge (BCNWR) is located 72.4 km northwest from downtown Austin near the town of Lago Vista and within the Edwards Aquifer recharge zone. Though the refuge encompasses approximately 18,615 ha, only about 9,637 ha are official refuge property. The landscape mostly consists of rugged terrain with oak-juniper thickets but eases into savannahs with patches of shin oak to the north. The refuge was primarily established to protect the breeding grounds of the GCWA and BCVI but is also designed to protect numerous subterranean karst invertebrates endemic to the area. In order to manage habitat within the refuge, prescribed burns are often used to reset succession. Very little recreation takes place on the refuge, primarily bird watching and hiking along 11 km of trails or controlled hunting of feral hogs and white-tailed deer for management purposes. (http://www.fws.gov/refuge/balcones_canyonlands/)

Balcones Canyonlands Preserve

In order to mitigate the impact of urban development on GCWA and BCVI breeding habitat, as well as several other endangered or at risk species, the U.S. Fish and Wildlife service issued a permit to the City of Austin and Travis County in 1996 under that Endangered Species Act. Known as the Balcones Canyonlands Conservation Plan (BCCP), the permit allows the 'take' of endangered species habitat in western Travis County for urban development in exchange for the creation of a habitat preserve system. With the help of other governmental, private, and non-profit agencies, the permit holders agree to fulfill their obligations stated in the BCCP by acquiring, protecting and managing a total of 12,313.8 ha of suitable habitat within twenty years of the issuance. Currently the Balcones Canyonlands Preserve (BCP) has approximately 92% of land required by the permit including two areas that will be used in this study. The South Lake Austin macrosite (SLAM) (1,257 ha) and the Upper Bull Creek macrosite (UBCM) (469 ha) are not open to the public except for limited deer hunting implemented for population control as well as occasional guided hikes.

(http://www.co.travis.tx.us/tnr/bccp/bc_preserve.asp)

APPENDIX C

Covariates of ψ and p , their units of measure, and a description. All distances measured from camera station coordinates.

$\psi(COV)$	Unit	Description
rds	meters/hectare	Paved public road density within 400 or 800 meters.
trls	meters/hectare	Trail, dirt road, and private drive density within 400 or 800 meters.
nat	proportion	Proportion of natural land cover within 400 or 800 meters.
alt	1, 0	Presence or absence of altered land cover (golf courses, agriculture, low density housing, etc.) within 400 or 800 meters.
urb	1, 0	Presence or absence of urban land cover within 400 or 800 meters.
area	hectares	Total area of natural habitat within two kilometers of sampling area property boundaries.
nearhab	meters	Straight line distance to nearest habitation, office building, or structure of daily human activity.
nearrd	meters	Straight line distance to nearest paved public road.
neartrl	meters	Straight line distance to nearest trail, dirt road, or private drive.
3km	proportion	Proportion of natural land cover within sampling area and extending three kilometers from sampling area boundaries.
$p(COV)$	Unit	Description
day	integer	Julian Day Number, continuous day of the year expressed as a whole number.
precip	1, 0	Any measurable precipitation for that day > 0mm.
temp	°C	Median temperature in degree Celcius.

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