SPATIAL ECOLOGY OF THE GRAY FOX (*UROCYON CINEREOARGENTEUS*) IN SOUTHEASTERN ARIZONA

by

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ABSTRACT

Where animals occur over space and time can inform effective conservation and management efforts for vector species of zoonotic diseases. Gray foxes (*Urocyon cinereoargenteus*) are a common and widespread species across their geographic range that can exist close to human disturbance. However, little is known about their space use in the southwestern United States, where they are a significant reservoir for a unique strain of the rabies virus. Gray foxes overlap with bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and striped skunks (*Mephitis mephitis*) across the southwestern United States. Space use by gray foxes has been impacted by presence of other mesocarnivores. How vector species interact with the landscape has a direct impact on the spread of diseases like rabies. Mesocarnivores were the source of over 90% of all reported rabies cases in 2016. We used remotely triggered cameras to detect gray foxes, bobcats, coyotes, and skunks and understand their habitat use in isolated vs. well-connected landscapes. We deployed 80 cameras, divided between two study sites in eastern Arizona, the Pinaleño and White Mountains, and stratified each in a random design by vegetation type. We collected data from June 2016 to August 2017, encompassing 19,700 camera trapping days. Gray foxes occupied an estimated 95.6% of sites. We ran a multi-species multi-season model to examine how occupancy of gray foxes changed. Our results showed that occupancy by coyotes, bobcats, and skunks had a negative influence on gray fox occupancy. We detected gray foxes across all sampled elevations and vegetation communities. Additionally, we used data acquired from VHF and GPS satellite collars on gray foxes in the White Mountains and Pinaleño Mountains of Arizona to compare habitat use, movement patterns, and home range requirements between a well-connected landscape and an isolated sky island. We sought to compare space use estimates between continuous and isolated forests using GPS and VHF technology. Average home range size was $3.78 \pm 2.74$ km² (SD) and gray foxes select for upper evergreen forests in the Pinaleño
Mountains and pine-juniper woodlands in the White Mountains. We were able to define specific vegetation communities used by adult gray foxes where oral vaccination efforts can be focused by rabies disease managers. Disease management for rabies epizootic events in the southwestern U.S. will benefit from our study of gray fox space use. Our results contribute greater insight into gray fox habitat use in isolated vs. well-connected landscapes. Understanding habitat use by gray foxes in Arizona can be used to inform rabies management across the broader southwestern United States.
CHAPTER 1: INTRODUCTION

Spatial Ecology

Space use is a fundamental characteristic of a species’ ecology that can provide insight into habitat use, resource use, and population dynamics. Animal space use across time can inform approaches for conservation and management (Aarts et al. 2008). When studied across an expansive geographic area, space use can be informative for habitat conservation, disease management, and interspecific relationships (DeYoung et al. 2009).

Rabies Management

Rabies is a prevalent zoonotic disease that remains a significant contemporary wildlife management and public-health challenge. Rabies, one of the oldest known viral diseases (Chipman 2014), affects the central nervous system of unvaccinated mammals that are exposed to the virus and is invariably fatal (World Health Organization 2017). Worldwide, more than 59,000 humans die from rabies each year, and approximately 5,500 cases of wildlife rabies are reported in the United States (U.S.) annually (Birhane et al. 2017; Chipman 2017). In the U.S. alone, $300 million is spent annually on rabies management programs (Chipman 2014). Over the past 30 years, rabies management has become more complex across the U.S. as wild animals have displaced the domestic dog (Canis familiaris) as the primary reservoir for the disease (USDA-APHIS-Wildlife Services 2015).

Mesocarnivores are the primary rabies reservoirs in the U.S. and were the source of over 90% of all reported rabies cases in 2016 (Ma et al. 2018). Rabies principally occurs in raccoons (Procyon lotor), striped skunks (Mephitis mephitis), gray foxes (Urocyon cinereoargenteus), and coyotes (Canis latrans) in the U.S. (Blanton et al. 2006; Birhane et al. 2017; Chipman 2017). Gray foxes are a substantial reservoir for rabies in the southwestern U.S. (Nelson et al. 2010;
Velasco-Villa et al. 2017) and harbor unique variants of the rabies virus in Arizona and Texas (USDA-APHIS-Wildlife Services 2015; Velasco-Villa et al. 2017). Two hundred seven gray foxes tested positive for rabies from 2001–2010 in Arizona alone (Arizona Department of Health Services 2011) with foxes collectively accounting for 6.4% of all national wildlife rabies cases in 2016 (Ma et al. 2018). Rabies epizootic events in foxes have occurred in Arizona, with the last occurring in Coconino County in 2008 and 2009 (Nelson et al. 2010). Currently, Arizona may be on the verge of another potential epizootic of the gray fox strain, as 34 foxes have tested positive for rabies in 2017 versus only 5 positive cases reported in foxes in 2016 (Arizona Department of Health Services 2018).

The rabies lyssavirus strain circulating in gray foxes in Arizona is a genetically distinct variant that occurs throughout northwest-central Mexico, Arizona, and New Mexico (Velasco-Villa et al. 2017). The geographic distribution of rabies-infected mammals elsewhere in the United States appears to be influenced by landscape features. Lack of physical barriers can increase gene flow (DeYoung et al. 2009) and length of epizootic events (Childs et al. 2001), which can greatly impact population dynamics of host species. Previous work on gray fox rabies management suggests that understanding gray fox ecology across an expansive geographic area can improve the efficiency of disease management plans (DeYoung et al. 2009).

**Study Organism**

Gray foxes are a widespread species that occurs throughout most of the contiguous United States, excluding some northeastern states, and ranges from southern Canada into northern South America (Hoffmeister 1986; Cypher 2003; Aldridge 2008). Gray foxes occupy a large variety of terrestrial vegetation communities in North America (Fritzell and Haroldson 1982; Hoffmeister 1986; Cypher 2003), indicating they are habitat generalists. In the
southwestern United States, gray foxes occur in brushy vegetation associated with rugged terrain and at elevations of 1,150-1,525 m (Fritzell and Haroldson 1982), including open desert-scrub, chaparral, oak or pinyon-juniper woodlands, and in ponderosa pine or Douglas fir (Hoffmeister 1986). However, the space use of gray foxes is still understudied in the southwestern United States (DeYoung et al. 2009). Most information on space use of gray foxes is inferred from studies in Texas, Utah, and California (Trapp and Hallberg 1975; Fritzell and Haroldson 1982; Hoffmeister 1986) but habitat use is not well documented (Hoffmeister 1986).

Gray foxes are sympatric with bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) throughout much of North America (Chamberlain and Leopold 2005). Chamberlain and Leopold (2005) documented extensive home range overlap among all three species in Mississippi, however, they documented that gray foxes maintained core areas that did not overlap substantially with those of bobcats and coyotes. This was most likely to avoid areas of high use by the larger carnivores (Chamberlain and Leopold 2005). Additionally, gray foxes have been documented to occur in similar vegetation communities as the striped skunk (*Mephitis mephitis*) in the Western United States (Hoffmeister 1986; Jones 2016) and have similar diets (Fritzell and Haroldson 1982; Wade-Smith and Verts 1982).

In 2016, skunks (*Mephitis sps.*) accounted for 21% of reported rabies cases in the United States (Ma et al. 2018). From 2016 to 2018 in Arizona, skunks accounted for 32.5% of wildlife rabies cases reported, gray foxes 18.9%, bobcats 2.4%, and coyotes 1.9% (Arizona Department of Health Services 2018). Space use by gray foxes is impacted by presence of other mesocarnivores (Chamberlain and Leopold 2005) and space use has a direct impact on the spread of diseases like rabies. Rabies is spread from direct contact between an infected host and a susceptible individual. How frequently individuals of the same and overlapping species
encounter one another has direct impacts for disease spillover and epizootic events. Prevalence of rabies in mesocarnivores has been well documented in Arizona, making the state an ideal place to examine how spatial overlap between mesocarnivores susceptible to the virus may influence the space use of gray foxes.

**Study Area**

We chose our study sites, the Pinaleño Mountains (32.70163°N, -109.87189°E) and the White Mountains (33.78512°N, -109.24785°E) in Arizona, for comparison due to their similarity in overall elevation and vegetation communities (Fritzell and Haroldson 1982; Hoffmeister 1986) and differences in habitat connectivity and disturbance levels (Leonard and Koprowski 2009). These mountains are dominated by chaparral, oak woodlands, pinyon-juniper, ponderosa pine, and mixed conifers including spruce-fir forest (Nichol 1937; Roccaforte et al. 2015). The Pinaleño Mountains are a mosaic of habitat patches due to insect outbreaks and fire. The White Mountains have also experienced large disturbance events, however these mountains exhibit a more connected landscape due to larger continuous forest patches (Roccaforte et al. 2015).
CHAPTER 2: PRESENT STUDY

This thesis is comprised of two manuscripts. The manuscripts can be found in Appendices A and B. Appendix A, formatted for the Journal of Mammalogy, entitled, “Occupancy and habitat use of Arizona gray fox (Urocyon cinereoargenteus),” assesses occupancy and habitat use of gray foxes (Urocyon cinereoargenteus) and the influence of other carnivores of potential importance in rabies management. Appendix B, formatted for Southwestern Naturalist, entitled, “Gray fox (Urocyon cinereoargenteus) space use in southeastern Arizona,” examines home range size and habitat use in isolated vs continuous landscapes. The following is a summary of the major findings.

Summary of Methods

We deployed 80 camera traps distributed equally between our two study sites in a stratified random design across vegetation communities. We paired each camera trap with a 10 m radius vegetation plot centered around the camera. At each plot we sampled diameter at breast height (DBH) and completed over- and understory measurements in all four cardinal directions at 5 m and 10 m from the base of the tree bearing the camera. We analyzed data from vegetation plots and camera traps using a hierarchical occupancy model across multiple seasons.

Additionally, we trapped and affixed radio collars to 17 adult gray foxes. We collected more than 218 hours of animal locations from VHF and GPS points. We calculated home range estimates, maximum distance moved, and habitat use for all individuals from which we were able to collect adequate spatial data. We used Welch’s modified two-sample t-test to compare these parameters across sexes, study sites, and data collection methods.
Summary of Results

Our assessment of seasonal occupancy showed that gray foxes occupied 95.6% of our sampling sites and that occupancy decreased when mesocarnivores were included in our models. We determined that average home range size for gray foxes was $3.78 \text{ km}^2 \pm 2.74$ (SD) and gray foxes selected for upper evergreen forests in the Pinaleño Mountains and pine-juniper woodlands in the White Mountains. Gray foxes moved a maximum of $2 \text{ km}$ over a $7$-h time interval on average.

Summary of Conclusions

Our study is one of the first to specifically examine gray fox space use in Arizona since the 1980s. Our finding that habitat use does not differ in isolated vs. continuous landscapes contributes to a greater understanding of gray fox ecology. Coyotes, bobcats, skunks, and foxes overlapped in our study. All four mesocarnivore species have been documented to tolerate human disturbance and use urban areas (Bateman and Fleming 2012). Rabies is a virulent disease that can easily spillover from one species into another (Velasco-Villa et al. 2017), making epizootic events difficult to manage. Rabies in gray foxes has important implications for population dynamics in foxes as well as for other species such as the endangered Mexican gray wolf (*Canis lupus baileyi*) in the White Mountains, Arizona. As habitat generalists that can exist close to humans, gray foxes could easily transfer rabies to livestock, pets, and even people. Oral rabies vaccination and trap-vaccinate-release programs can be successful in combating rabies in mesocarnivores across urban and rural areas (Theimer et al. 2017). Understanding what vegetation communities, elevation, and general landscape features that are more likely to be occupied by gray foxes and other rabies susceptible wildlife can increase efficiency for disease management techniques that will protect wildlife populations, domestic animals, and humans.
LITERATURE CITED


APPENDIX A: Occupancy and habitat use of Arizona gray fox (Urocyon cinereoargenteus)
Amanda M. Veals, John L. Koprowski, Kurt C. VerCauteren, and David L. Bergman

(In the format of Journal of Mammalogy)
Spatial and temporal distributions of wildlife can inform effective conservation and management efforts for vector species of zoonotic diseases. Gray foxes (*Urocyon cinereoargenteus*) are a common and widespread species across their geographic range that can exist in proximity to human activities. However, little is known about their space use in the southwestern United States where they are an important reservoir for a unique strain of the rabies lyssavirus. Gray foxes overlap with bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and striped skunks (*Mephitis mephitis*) across the southwestern United States. Space use by gray foxes can be impacted by presence of other mesocarnivores. How vector species interact with the landscape and each other might influence the spread of diseases like rabies. We used remotely triggered cameras to survey gray foxes, bobcats, coyotes, and skunks to assess their habitat use in isolated vs. well-connected
landscape. We deployed 80 cameras, divided between two study sites in eastern Arizona, the Pinaleño and White Mountains, and stratified each area by vegetation type. We collected data from June 2016 to August 2017, encompassing 19,700 camera trapping days. Gray foxes occupied an estimate of 95.6% (± 0.17 SE) of sites and we detected gray foxes across all sampled elevations and vegetation communities. We ran a multi-species multi-season occupancy model to examine how occupancy of gray foxes changed through time. Occupancy at sites by coyotes, bobcats, and skunks had a negative influence on gray fox occupancy. Our findings suggest that gray foxes are habitat generalists that overlap in space with other mesocarnivores, which could affect rabies dynamics in Arizona. We suggest focusing efforts to distribute oral vaccine baits and trapping during an outbreak in areas of overlap between these mesocarnivores. An understanding of habitat use by gray foxes in Arizona can be used to inform rabies management across the broader southwestern United States.

Keywords: Disease management, rabies, spatial use

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A species’ distribution across the landscape can provide insight into habitat and resource use (Bailey and Adams 2005). Science-based approaches to determine where animals occur in space and time can inform effective species conservation and management (Aarts et al. 2008), especially when studies encompass expansive geographic areas. Occupancy modeling is a time- and cost-effective method to study species distribution and factors that determine habitat use (Bailey and Adams 2005). Additionally, enhanced knowledge of wildlife ecology can inform disease etiology and transmission rates for zoonotic diseases (Alexander et al. 2012). By examining habitat use of a vector species for zoonotic diseases, management strategies for both the disease and host species can be improved (Birhane et al. 2017). Mesocarnivores that are
widespread and far ranging can often be both vectors and reservoirs for prevalent zoonotic diseases, which make this group of organisms ideal models to understand how species’ distribution across space and time can inform disease management (DeYoung et al. 2009).

Rabies is a prevalent zoonotic disease that remains a significant contemporary wildlife management and public-health challenge. Rabies, one of the oldest known viral diseases (Chipman 2014), affects the central nervous system of unvaccinated mammals that are exposed to the virus and is invariably fatal (World Health Organization 2017). Worldwide, more than 59,000 humans die from rabies each year, and approximately 5,500 cases of wildlife rabies are reported in the United States (U.S.) annually (Birhane et al. 2017; Chipman 2017). In the U.S. alone, $300 million is spent annually on rabies management programs (Chipman 2014). Over the past 30 years, rabies management has become more complex across the U.S. as wild animals have displaced the domestic dog (Canis familiaris) as the primary reservoir for the disease (USDA-APHIS-Wildlife Services 2015).

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occurs in Coconino County in 2008 and 2009 (Nelson et al. 2010).Currently, Arizona may be on the verge of another potential epizootic of the gray fox strain, as 34 foxes have tested positive for rabies in 2017 versus only 5 positive cases reported in foxes in 2016 (Arizona Department of Health Services 2018).

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Gray foxes are a widespread species that occurs throughout most of the contiguous United States, excluding some northeastern states, and ranges from southern Canada into northern South America (Hoffmeister 1986; Cypher 2003; Aldridge 2008). Gray foxes occupy a large variety of terrestrial vegetation communities in North America (Fritzell and Haroldson 1982; Hoffmeister 1986; Cypher 2003), indicating they are habitat generalists. In the southwestern United States, gray foxes occur in brushy vegetation associated with rugged terrain and at elevations of 1,150-1,525 m (Fritzell and Haroldson, 1982), including open desert-scrub, chaparral, oak or pinyon-juniper woodlands, and in ponderosa pine or Douglas fir (Hoffmeister, 1986). However, the space use of gray foxes is still understudied in the southwestern United States (DeYoung et al. 2009). Most information on space use of gray foxes is inferred from
studies in Texas, Utah, and California (Trapp and Hallberg 1975; Fritzell and Haroldson 1982; Hoffmeister 1986) but habitat use is not well documented (Hoffmeister 1986).

Gray foxes are sympatric with bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) throughout much of North America (Chamberlain and Leopold 2005). Home range overlap was extensive among all three species in Mississippi, however, gray foxes maintained core areas that did not overlap substantially with those of bobcats and coyotes (Chamberlain and Leopold 2005). This suggests avoidance of areas of high use by the large carnivores (Chamberlain and Leopold 2005). Additionally, gray foxes occur in similar vegetation communities as the striped skunk (*Mephitis mephitis*) in the western United States (Hoffmeister 1986; Jones 2016) and have similar dietary needs as skunks (Fritzell and Haroldson 1982; Wade-Smith and Verts 1982).

In 2016, skunks (*Mephitis sps.*) accounted for 21% of reported rabies cases in the United States (Ma et al. 2018). From 2016 to 2018 in Arizona, skunks accounted for 32.5% of wildlife rabies cases reported, gray foxes 18.9%, bobcats 2.4%, and coyotes 1.9% (Arizona Department of Health Services 2018). Space use by gray foxes can be impacted by presence of other mesocarnivores (Chamberlain and Leopold 2005) and space use has a direct impact on the spread of diseases like rabies. Rabies is spread from direct contact between an infected host and a susceptible individual. How frequently individuals of the same and overlapping species encounter one another has direct impacts for disease spillover and epizootic events. Prevalence of rabies in mesocarnivores is high in Arizona, making the state an ideal place to examine how spatial overlap between mesocarnivores susceptible to the virus may influence the space use of gray foxes.

We were interested in the distribution and habitat use of gray foxes in Arizona where the unique variant of rabies is endemic. Our study was conducted in the Pinaleño Mountains and the
White Mountains of southeastern Arizona to examine differences between continuous landscapes and isolated sky islands.

Southeastern Arizona has a large, intact mesocarnivore guild and our two study sites had a diversity of available vegetation communities. The Madrean Sky Island ecosystems that we worked in have high levels of biological diversity (Coronel-Arellano et al. 2018). Systems with greater biological diversity may experience a dilution effect on prevalence of zoonotic diseases in vector species (Ostfeld and Keesing 2000), which could have implications for spillover between mesocarnivore species that are susceptible to rabies. Zoonoses stemming from wildlife vectors is an increasingly important area of concern for both human and animal health (Alexander et al. 2012). Vector species ecology can provide an important baseline for disease management strategies (DeYoung et al. 2009; Alexander et al. 2012), especially in biologically diverse ecosystems and heterogeneous landscapes, as we suspect with gray foxes in southeastern Arizona.

We compared distribution through occupancy modeling of gray foxes in these two populations to determine if habitat use differed between landscapes of varying fragmentation. Additionally, we examined occupancy of three other mesocarnivores of importance for rabies and interspecific competition with gray foxes: coyotes, bobcats, and skunks (*Mephitis* sps. and *Conepatus leuconotus*). We wanted to examine if gray fox occupancy at sites is influenced by presence of these mesocarnivores.

To make informed management decisions in the future for rabies disease management, understanding how gray foxes use the landscape is important to control the spread of the virus during periodic epizootics. The distribution of gray foxes in Arizona can be used to inform state-specific disease mitigation through targeted vaccine distribution and removal. Increasing our
understanding of spatial overlap with other mesocarnivores will provide insight into the potential for rabies to spillover into other hosts.

**MATERIALS AND METHODS**

*Study Area*—We selected the Pinaleño Mountains (32.70163°N, -109.87189°E) and the White Mountains (33.78512°N, -109.24785°E) for comparison due to their similarity in overall elevation and vegetation communities (Vahle 1978; Fritzell and Haroldson 1982; Hoffmeister 1986), and their differences in habitat connectivity and disturbance levels (Leonard and Koprowski 2009; Sanderson and Koprowski 2009). The Pinaleño Mountains are fragmented by roads and disturbance events including large scale fires and insect damage (O’Connor et al. 2014). The Pinaleño Mountains comprise only 780 km² in forested area and are considered a sky island within the Madrean Sky Island Complex (Warshall 1995). The White Mountains have also experienced large disturbance events from fires and insect damage, and have many roads, however, exhibit a more connected landscape due to larger continuous forest patches (Warshall 1995; Zugmeyer and Koprowski 2008). The White Mountains are approximately 13,000 km² of continuous forest. The vegetation across both mountain ranges is composed of cork-bark fir (*Abies lasiocarpa* var. *arizonica*), Douglas fir, Engelmann spruce (*Picea engelmanii*), ponderosa pine, quaking aspen (*Populus tremuloides*), southwestern white pine (*Pinus strobiformis*) and white fir (*Abies concolor*; Vahle 1978; Sanderson and Koprowski 2009).

*Camera Trapping*—We deployed 80 camera traps (HD Trophy model; Bushnell Inc., Overland Park, Kansas), 40 within each of our two study sites as a stratified random sample by vegetation community to evaluate how heterogeneity in available vegetation communities within our study areas could influence gray fox habitat use (Garton et al. 2012; Rovero et al. 2013). We used Geographic Information Systems (GIS; ESRI, Redlands, CA) to randomize camera points
across vegetation communities. Vegetation communities were classified as polygons and defined by the species or genera of greatest abundance, based on the uppermost canopy of the plant community (USDA-U.S. Forest Service 2016). We attached cameras to trees at random locations spaced > 1.0 km apart. The number of cameras allocated per stratum was proportional to the percentage of area each dominance type covered within each study area. We kept cameras active in each location for approximately 1 year to collect multi-seasonal data across annual weather patterns.

Vegetation Sampling—We placed a 10-m-radius vegetation plot centered around each camera. We surveyed vegetation communities present across both mountain ranges, including: upper evergreen forest, ponderosa pine, pine-oak-juniper woodlands, and grass forb (USDA-U.S. Forest Service 2016). At each plot, we surveyed diameter at breast height (DBH) of all living woody plants to categorize as shrubs (woody plants < 10 cm DBH) or trees (> 10 cm DBH; Doumas and Koprowski 2013) and recorded the number of woody plants within each category. We also recorded the number of dead trees (logs/snags > 2 m long and 20 cm in diameter; Doumas and Koprowski 2013). We completed over- and understory measurements in all four cardinal directions at 5 m and 10 m out from the base of the tree bearing the camera. We used a spherical densiometer and the Strickler method to estimate canopy cover (Strickler 1959). We used a cover pole measuring 2.5 cm x 200 cm marked every 10 cm to measure understory density (Griffith and Youtie 1988). We noted any obscuring vegetation taller than the pole as > 2 m. We measured tree species richness and used the Shannon index to calculate diversity of tree species at each plot.

Analysis—We used dynamic occupancy models to identify covariates that explained variation in initial occupancy (ψ), local colonization (γ) and local extinction (ε) probabilities
between seasons, and detection probability (p) as developed by MacKenzie et al. (2002, 2003) and MacKenzie and Bailey (2004). We identified six seasons as primary sampling periods (MacKenzie et al. 2003), which we classified by monthly precipitation and temperature for 2016-2017. We classified January, February, and March as winter/spring, a cold and wet season; April, May, and June as spring/summer, a relatively hot and dry season; July, August, and September as monsoon, a hot and wet season; and October, November, and December as fall/winter, a relatively cold and dry season (Thompson 2016). Our six primary sampling periods included: spring/summer 2016, monsoon 2016, fall/winter 2016, winter/spring 2017, spring/summer 2017, and monsoon 2017.

We used the unmarked package (Fiske et al. 2011) in R (R Development Core Team 2016) to build hierarchical models to examine single-species occupancy of gray foxes, coyotes, bobcats, and skunks across a multi-seasonal framework. Vegetation characteristics (i.e., canopy cover, understory height, tree diversity, tree richness, and DBH), elevation, vegetation community type, and study site were used as model covariates to evaluate potential effects on occupancy, local colonization and local extinction. Season and daily average temperature were included as covariates for detection probability. We used ΔAICc scores of > 2 to distinguish among models.

We wanted to examine how occupancy by coyotes, bobcats, and skunks influenced occupancy by gray foxes by testing a set of multi-season, multi-species occupancy candidate models. We used the top single-species occupancy model for each of the respective mesocarnivores (Table 1) and then predicted the site-specific psi estimate using the predict function in R. Then we used these estimates of psi for coyotes, bobcats, and skunks as site-level covariates in an unmarked multi-seasonal occupancy frame for gray foxes.
We used two-sample t-tests to compare vegetation characteristics and elevation among study sites (Leonard and Koprowski 2009).

**Results**

We surveyed 80 sites over a period of 446 days between 8 June 2016 and 27 August 2018 for a total of 35,680 trap days. We detected gray foxes on 606 days, skunks on 584 days, and bobcats on 161 days across both study sites. We detected coyotes on 264 days but only in the White Mountains. Gray foxes, bobcats, and skunks were detected across the entire range of elevations that we surveyed (1,530 to 2,985 m). Coyotes were detected across the entire range of elevations that we surveyed in the White Mountains (2,180 to 2,805 m). Gray foxes, bobcats, and skunks were detected across all available vegetation communities. Coyotes were never detected in pine-oak-juniper or upper pine-oak, consequently, these vegetation communities were available in the Pinaleño Mountains where the species was never detected.

Detection probability was positively influenced by temperature for coyotes whereas for skunks and gray foxes, detection probability was negatively influenced by temperature (Table 1). Gray foxes were more likely to be detected in the monsoon season of 2016 and the winter/spring, spring/summer, and monsoon seasons of 2017 (Table 1). Skunks were more likely to be detected in the monsoon season of 2016, and the spring/summer and monsoon seasons of 2017 (Table 1). Bobcats were more likely to be detected in the monsoon season of 2016 than any other season whereas with coyotes were more likely to be detected in the winter/spring of 2017 than any other season (Table 1).

Initial occupancy for coyotes was influenced positively by vegetation type, canopy connectivity, understory height, and DBH, whereas elevation, canopy cover, diversity of tree species, and richness of tree species had a negative influence on initial occupancy (Table 1).
Study site, vegetation type, DBH, diversity of tree species, and richness of tree species had a negative influence on initial occupancy for bobcats whereas elevation and understory height had a positive influence on initial occupancy (Table 1). Initial occupancy for skunks was positively influenced by study site, vegetation type, canopy cover, canopy connectivity, understory height, DBH, diversity of tree species, and richness of tree species but negatively influenced by elevation (Table 1). Gray fox initial occupancy was influence by only two covariates; vegetation type and study site had a negative influence on initial occupancy of gray foxes (Table 1).

Initial site occupancy for all four species was influenced by study site and vegetation community, but vegetation differed between study sites. The Pinaleño Mountains were dominated by upper evergreen forest (62.5%) whereas the White Mountains were more heterogenous, composed of ponderosa pine woodlands (42.5%), upper evergreen forest (30.0%), and pine-oak-juniper woodlands (25.0%).

Temperature had a negative influence on the colonization and extinction rates for skunks and bobcats (Table 1). Colonization rate was negatively influenced by temperature for coyotes, but a positive influence on extinction rate for the species (Table 1). Elevation had a negative influence on the colonization rate for coyotes and gray foxes but had a positive influence on colonization rate for skunks (Table 1). Extinction rate was positively influenced by elevation for gray foxes, skunks, and coyotes (Table 1).

Vegetation and structural characteristics varied between our two study sites. We found significant differences in elevation ($t_{50.48} = 2.061, p = 0.012$) and canopy cover ($t_{50.37} = 1.012, p = 0.032$) between our two study sites. Understory height ($t_{78.61} = -0.637, p = 0.526$) and DBH ($t_{77.83} = -4.188, p = 0.816$) did not differ between the Pinaleño Mountains and the White Mountains. Our top occupancy model did not include these covariates as significant for gray fox occupancy.
These vegetation covariates were included in our initial models but through model selection (AIC > 2) our top models demonstrate that these covariates did not influence occupancy or detection probability (Table 1).

Gray foxes occupied 95.6% (± 0.17 SE) of sites across the White and Pinaleño Mountains in southeastern Arizona (Table 1). Using this model as a baseline, we compared how our occupancy estimate changed when we includedψ estimates for coyotes, bobcats, and skunks as site-level covariates in our multi-species multi-season model. We found that the original model that did not include occupancy estimates for any other species was still our top model (Table 2). Three other models had AIC scores with a difference of two from our top model: skunk occupancy, bobcat occupancy, and coyote occupancy. Site occupancy of the other three mesocarnivores had negative relationships with occupancy for gray foxes. Including psi estimates for coyotes, bobcats, and skunks into our models decreased the psi estimate produced for gray foxes (Table 2). When mesocarnivore occupancy was included in the model, gray fox occupancy decreased. Gray fox occupancy at our sites decreased from 95.6% (± 0.17 SE) to 93.5% (± 0.22 SE) when skunks were present, 86.6% (± 0.15 SE) when bobcats were present, and 78.3% (± 0.24 SE) when coyotes were present.

**DISCUSSION**

Our study is the first to specifically examine gray fox occupancy and habitat use in Arizona since the 1980s (Trapp and Hallberg 1975; Hoffmeister 1986). Arizona gray foxes are habitat generalists able to persist in a wide variety of vegetation communities (Fritzell and Haroldson 1982; Hoffmeister 1986). We found that foxes occupy a diverse range of vegetation communities, including ponderosa pine stands, evergreen forests, and pine-oak-juniper woodlands.
We compared the Pinaleño and White Mountains to gain insight into the impacts that habitat fragmentation and isolation could have on the distribution of gray foxes. We found that occupancy was not different between the two mountain ranges, which suggests that foxes are less susceptible to the negative impacts of habitat loss and fragmentation than species with more habitat specialization (Bender et al. 1998; Devictor et al. 2008). Species that are more tolerant of expanding urbanization and human population densities are predicted to have a greater importance in future zoonotic disease management (Daszak et al. 2000). As habitat generalists that can exist close to human disturbance (Crooks 2002), gray foxes would remain a considerable concern as a rabies vector across the United States. By understanding where vector species, such as the gray fox, are on the landscape and what factors may contribute to their habitat use, managers can increase efficiency for disease management (Mills and Childs 1998).

Climate and resource availability can change drastically across seasons, particularly in the Madrean Archipelago where a wide range of microclimates occur in close proximity due to large elevation gradients (Thompson 2016). Because climate and resource availability can change markedly across seasons, many species shift their distributions in response to these changes (Thompson 2016). We found seasonal differences in detection of mesocarnivores at our sites. Daily average temperature influenced the seasonal colonization and extinction rates of coyotes, skunks, and bobcats. These patterns suggest seasonal changes in the distributions of mesocarnivores. Food resources often have a seasonal availability and may be one of the most influential factors governing seasonal occupancy of animals (Thompson 2016). The seasonal changes in occupancy of the four mesocarnivores, likely reflects temporal variation in a wide range of food resources. The diet and resource requirements for gray foxes can overlap significantly with bobcats and coyotes (Gittleman and Harvey 1982, Neale and Sacks 2001) as
well as skunks (Fritzell and Haroldson 1982; Wade-Smith and Verts 1982; Jones 2016).
Considering how distribution of foxes change in relation to species that compete for resources
and influence space use (Neale and Sacks 2001; Chamberlain and Leopold 2005; Jones 2016)
brings a more holistic approach to occupancy modeling.

Gray fox occupancy decreased at our sites when we accounted for occupancy of other
mesocarnivores. Although gray fox occupancy decreased when skunks occupied sites, it was a
minimal difference (95.6% to 93.5%). However, bobcats and coyotes had greater impact on gray
fox occupancy. Gray fox occupancy decreased to 86.6% when bobcats were present and 78.3%
when coyotes were present. Space use by gray foxes can be impacted by presence of bobcats and
coyotes (Neale and Sacks 2001; Chamberlain and Leopold 2005). Here we see similar changes in
occupancy, likely due to antagonistic relationships between bobcats and coyotes with gray foxes.

We saw that skunk occupancy was the second best model for explaining gray fox
occupancy. Skunk occupancy had a negative relationship with gray fox occupancy, however,
gray foxes still occupied 93.5% of our sites even when skunks were present. Where we detected
skunks, that site was likely occupied by gray foxes as well. This is most likely due to overlap in
diet and habitat use between the two species (Fritzell and Haroldson 1982; Wade-Smith and
Verts 1982; Jones 2016). Gray foxes and striped skunks are two of the largest reservoirs for
rabies in Arizona and many recent outbreaks have occurred in both species in the 2000s
(Theimer et al. 2017a). The spatial overlap between gray foxes and skunks could have serious
implications for rabies management in the State. There is a higher probability of gray foxes and
skunks encountering each other on the landscape, which could lead to a higher rate of disease
spillover between the two species.
Coyotes, bobcats, skunks, and gray foxes overlapped in our study. These four species have the potential to interact with not just each other but pets, livestock and people. All four mesocarnivore species have been documented to tolerate human disturbance and use urban areas (Bateman and Fleming 2012). Rabies is a virulent disease that can easily spillover from one species into another (Velasco-Villa et al. 2017), making epizootic events difficult to manage. Rabies in gray foxes has important implications for population dynamics in foxes as well as for other species such as the endangered Mexican gray wolf (Canis lupus baileyi) in the White Mountains, Arizona. As habitat generalists that can exist close to humans, gray foxes could easily transfer rabies to livestock, pets, and even people. Oral rabies vaccination (ORV) and trap-vaccinate-release programs can be successful in combating rabies in mesocarnivores across urban and rural areas (Rosatte et al 1992; Theimer et al. 2017b).

Coyotes, bobcats and skunks negatively influenced occupancy of gray foxes and the presence of these mesocarnivores should be considered in both proactive and reactive strategies for controlling the spread of rabies in Arizona. These four species overlapped across vegetation communities, elevations, and mountain ranges that we examined. Additionally, mesocarnivores overlap in diet with foxes, which could impact uptake rates of oral vaccines by gray foxes. Oral rabies vaccines for the Arizona-gray fox variant could reach other mesocarnivores that co-occur in targeted areas, potentially decreasing then number of individuals susceptible to rabies that overlap with gray foxes. Consequently, gray foxes may have reduced access to oral vaccine baits in areas where they significantly overlap with larger carnivores such as coyotes and bobcats.

Seasonal variations in temperature and food availability is most likely playing a key factor in the distribution of gray foxes, coyotes, bobcats, and skunks in our study sites. We recommend that rabies managers consider delivering oral vaccine baits onto the landscape when
natural food resources are scarce, particularly in the two drier seasons in Arizona (spring-summer and fall-winter). Competition for resources is most likely higher during these times of year, however, animals may be more likely to find and eat baits in times of low food availability. Distribution across space and time play a role in intra- and interspecific interactions and therefore disease spread.

Understanding what vegetation communities, elevations, and general landscape features that are more likely to be occupied by gray foxes and other rabies susceptible wildlife at certain times of the year, can increase efficiency and minimize costs for disease management techniques. Proactive rabies management that considers spatial overlap and resource competition among rabies vectors will likely have a higher success rate for protecting wildlife populations, domestic animals, and humans. Disease management strategies in Arizona could be better informed with studies focused on oral vaccine uptake and immunization potential in gray foxes and other mesocarnivores. We recommend management efforts that are targeting gray foxes to focus on areas where foxes have highest site occupancy.

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**Literature Cited**


Table 1. Estimated initial occupancy ($\psi$), local colonization ($\gamma$), local extinction ($\varepsilon$), and detection probability ($p$) of the top-ranked models for gray foxes, coyotes, bobcats, and skunks in the Pinaleño and White Mountains of southeastern Arizona.

<table>
<thead>
<tr>
<th>Species</th>
<th>Top Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gray Fox</td>
<td>$\psi$ (study site + vegetation type)</td>
</tr>
<tr>
<td></td>
<td>$\gamma$ (study site + vegetation type + elevation)</td>
</tr>
<tr>
<td></td>
<td>$\varepsilon$ (study site + vegetation type + elevation)</td>
</tr>
<tr>
<td></td>
<td>$p$ (season + temperature)</td>
</tr>
<tr>
<td>Coyote</td>
<td>$\psi$ (vegetation type + elevation + canopy cover + connectivity + understory + DBH + richness + diversity)</td>
</tr>
<tr>
<td></td>
<td>$\gamma$ (vegetation type + elevation + temperature)</td>
</tr>
<tr>
<td></td>
<td>$\varepsilon$ (vegetation type + elevation + temperature)</td>
</tr>
<tr>
<td></td>
<td>$p$ (vegetation type + season + temperature)</td>
</tr>
<tr>
<td>Bobcat</td>
<td>$\psi$ (study site + vegetation type + elevation + understory + DBH + richness + diversity)</td>
</tr>
<tr>
<td></td>
<td>$\gamma$ (study site + temperature)</td>
</tr>
<tr>
<td></td>
<td>$\varepsilon$ (study site + temperature)</td>
</tr>
<tr>
<td></td>
<td>$p$ (vegetation type + season)</td>
</tr>
<tr>
<td>Skunk</td>
<td>$\psi$ (study site + vegetation type + elevation + canopy cover + connectivity + understory + DBH + richness + diversity)</td>
</tr>
<tr>
<td></td>
<td>$\gamma$ (study site + vegetation type + elevation + temperature)</td>
</tr>
<tr>
<td></td>
<td>$\varepsilon$ (study site + vegetation type + elevation + temperature)</td>
</tr>
<tr>
<td></td>
<td>$p$ (vegetation type + season + temperature)</td>
</tr>
</tbody>
</table>
Table 2. Multi-species occupancy models for gray foxes in the Pinaleño and White Mountains of southeastern Arizona. The “coyote”, “bobcat”, and “skunk” covariates are occupancy estimates for each species. Covariates for $\gamma$, $\varepsilon$, and $p$ were identical across all candidate models; covariates included in the original model are the same used for all other candidate models. Change in Akaike information criterion ($\Delta$AIC) is the difference in AIC values between each model with the lowest AIC model.

<table>
<thead>
<tr>
<th>Top Models</th>
<th>$\psi$ (study site + vegetation type)</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Original: Gray Fox</td>
<td>$\psi$ (study site + vegetation type)</td>
<td>4409.24</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>$\gamma$ (study site + vegetation type + elevation)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\varepsilon$ (study site + vegetation type + elevation)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p$ (season + temperature)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Skunk Occupancy</td>
<td>$\psi$ (study site + vegetation type + skunk)</td>
<td>4409.64</td>
<td>0.40</td>
</tr>
<tr>
<td>Bobcat Occupancy</td>
<td>$\psi$ (study site + vegetation type + bobcat)</td>
<td>4410.97</td>
<td>1.73</td>
</tr>
<tr>
<td>Coyote Occupancy</td>
<td>$\psi$ (study site + vegetation type + coyote)</td>
<td>4411.24</td>
<td>2.00</td>
</tr>
<tr>
<td>Bobcat + Skunk Occupancy</td>
<td>$\psi$ (study site + vegetation type + bobcat + skunk)</td>
<td>4411.39</td>
<td>2.15</td>
</tr>
<tr>
<td>Coyote + Skunk Occupancy</td>
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<td>$\psi$ (study site + vegetation type + coyote + bobcat + skunk)</td>
<td>4413.39</td>
<td>4.15</td>
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</tbody>
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APPENDIX B: GRAY FOX (*UROCYON CINEROARGENTEUS*) SPACE USE IN SOUTHEASTERN ARIZONA

Amanda M. Veals, John L. Koprowski, Kurt C. VerCauteren, and David L. Bergman

(In the format of *Southwestern Naturalist*)
GRAY FOX (*UROCYON CINEREOARGENTEUS*) SPACE USE IN SOUTHEASTERN ARIZONA

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ABSTRACT—Gray foxes (*Urocyon cinereoargenteus*) are considered a widespread and common species in the southwestern United States; however, their spatial ecology is poorly known. We used data acquired from VHF and GPS satellite collars on gray foxes in the White Mountains and Pinaleño Mountains of Arizona to compare habitat use, movement patterns, and home range requirements. We sought to compare space-use estimates between continuous and isolated landscapes. Average home range size was 3.78 km² ± 2.74 (SD) and gray foxes used upper evergreen forests in the Pinaleño Mountains and pine-juniper woodlands in the White Mountains. We were able to define specific vegetation communities used by adult gray foxes where oral vaccination efforts can be focused for rabies management. Disease management for rabies epizootic events in the southwestern U.S. will benefit from our study of gray fox space use.

RESUMEN—El Zorro gris (*Urocyon cinereoargenteus*) es considerada como una especie ampliamente distribuida y común en el Suroeste de Estados Unidos, aunque su ecología espacial no ha sido estudiada a detalle. A través de collares de telemetría VHF y GPS instalados en zorros grises en las White Mountains y Pinaleño Mountains localizadas en Arizona, se comparó selección de hábitat, patrones de movimiento y rango de hogar entre un paisaje con alta conectividad y un paisaje aislado en las Sky Islands. Buscamos comparar el uso del espacio estimado entre bosques continuos y aislados usando tecnología GPS y VHF. El rango de hogar promedio fue de 3.78 km² (± 2.74). Los zorros grises seleccionaron bosques siempreverdes en Pinaleño Mountains y los bosques de Pino-Junípero en White Mountains.
Space use is a fundamental characteristic of a species’ ecology that can provide insight into habitat use, resource use, and population dynamics. Animal space use across time can inform approaches for conservation and management (Aarts et al., 2008). Especially when studied across an expansive geographic area, space use can be informative for habitat conservation, disease management, and interspecific relationships (DeYoung et al., 2009).

Gray foxes (*Urocyon cinereoargenteus*) are a widespread species that occurs throughout most of the contiguous United States, except for some northeastern states; they range from southern Canada into northern South America (Hoffmeister, 1986; Cypher, 2003; Aldridge, 2008). Gray foxes occupy a large variety of terrestrial vegetation communities in North America (Cypher, 2003), but thrive in a variety of areas including mixed woodland/agricultural landscapes in the Midwest, deciduous hardwoods in the East, and juniper woodlands in the West (Aldridge, 2008). In the southwestern United States, gray foxes occur in brushy vegetation associated with rugged terrain and at elevations of 1,150-1,525 m (Fritzell and Haroldson, 1982), including open desert-scrub, chaparral, oak or pinyon-juniper woodlands, and in ponderosa pine (*Pinus ponderosa*) or Douglas fir (*Pseudotsuga menziesii*; Hoffmeister, 1986). Gray fox home ranges vary greatly across vegetation and season (Cypher, 2003; Aldridge, 2008), often influenced by food abundance, habitat quality, interspecific competition, and presence of young (Aldridge, 2008). However, the spatial ecology of gray foxes is relatively understudied in the southwestern United States (DeYoung et al., 2009) and in Arizona their habitat use is not well documented (Hoffmeister 1986). Most information on gray fox habitat use and home range in the western United States is inferred from studies in Utah, Texas, and California (Trapp and Hallberg, 1975; Fritzell and Haroldson, 1982; Hoffmeister, 1986; DeYoung et al., 2009).

In Arizona, and the broader southwestern United States, gray foxes are a significant reservoir for rabies (Nelson et al. 2010; Velasco-Villa et al. 2017). The rabies lyssavirus strain circulating in Arizona gray fox populations is a genetically distinct variant that occurs throughout northwest-central Mexico, Arizona, and New Mexico (Velasco-Villa et al. 2017). Previous work on gray fox rabies management suggests that understanding gray fox ecology across an expansive geographic area can improve the efficiency of disease management plans (DeYoung et al. 2009).

We evaluated spatial data collected from GPS/VHF collars to understand home range and habitat use of gray foxes across varying terrain types, levels of habitat connectivity, and seasonal rainfall patterns that characterize the high elevation forests of Arizona. Our objectives were to, 1) report seasonal home ranges for gray foxes in heterogenous landscapes; 2) gain insights into habitat use by an important rabies vector; and 3) provide direction for rabies management in Arizona for oral vaccination distribution, trapping/removal efforts, and public health awareness campaigns.

**MATERIALS AND METHODS—Study Area**—We chose our study sites, the Pinaleño Mountains (32.70163°N, -109.87189°E) and the White Mountains (33.78512°N, -109.24785°E), for comparison due to their similarity in overall elevation and vegetation communities (Fritzell and Haroldson, 1982; Hoffmeister, 1986) and differences in habitat connectivity and disturbance levels (Leonard and Koprowski, 2009). These mountains are dominated by chaparral, oak woodlands, pinyon-juniper, ponderosa pine, and mixed conifers including spruce-fir forest (Nichol, 1937; Roccaboforte et al., 2015). The Pinaleño Mountains are a mosaic of habitat patches due to insect outbreaks and multiple large fires. The White Mountains have also experienced
large disturbance events, though they exhibit a more connected landscape due to larger continuous forest patches (Roccaforte et al., 2015).

**Trapping**—We trapped gray foxes in frameless body, guillotine door metal traps (28x51 cm, 25x48 cm, 23x46 cm, 20x43 cm; all 92 cm in length; Caging Bobcats, Barstow, California) over the course of 700 trap nights. Traps were baited with food bait (canned sardines) and a scent lure (Powder River Cat Call; Minnesota Trapline Products, Pennock, MN). We transferred captured foxes quickly to a heavy dark-colored, cloth cone for handling (McCoglin et al., 2018). We determined sex/age/reproductive condition and recorded body measurements. A numbered, 0.48x2.38 cm, ear tag (Model 1005-3; National Band & Tag Co., Newport, Kentucky) was affixed in the pinna of each ear. Adult animals were then fitted with a GPS/VHF collar (MiniTrack160; Lotek Wireless Inc., Ontario, Canada) and released at the site of capture. We deployed 17 radio collars (MiniTrack160 GPS/VHF collars; Lotek Wireless Inc., Ontario, Canada) on 10 female and 7 male adult gray foxes.

All field work was conducted in accordance with the American Society of Mammalogists guidelines (Sikes et al., 2016) and approved by the University of Arizona’s Institutional Animal Care and Use Committee (IACUC protocol #14-504).

**Radio Telemetry**—More than 218 hours were expended to collect animal locations from VHF and GPS points. We located animals between 1000 h-1600 h each day using the VHF signal. We used single-person biangulation, with interbearing intervals < 10 min. of one another, to estimate animal location. Additionally, collars collected a GPS point every seven hours which we downloaded directly off collars periodically. GPS points from three collars were successfully downloaded and biangulations with VHF was successful on 14 foxes (Table 1). We acquired data from two foxes with both GPS/VHF and two foxes had no data collected from either GPS or VHF signals.

**Home-Range Analysis**—We used Location of a Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary) to estimate animal locations via bearing intersections using the “best biangulation” function. We calculated minimum convex polygons (MCP) using the Spatial Analyst tool and Animal Movement extensions (Hooge and Eichenlaub, 1997) in ArcView v.3.3 (ESRI; Redlands, CA) as well as maximum distance moved between points. We used GPS fixes collected from collared foxes to generate home range estimates of the two populations of gray foxes. We used Ranges 9 (Anatrack Ltd.; Kenward et al., 2014) to generate 95% fixed-kernel home-range estimates (KDE) via least-squares cross validation of the smoothing parameter (Leonard and Koprowski, 2009) and determined maximum distance moved between points. We eliminated individuals with < 70 data points from our analysis; this left us with a sample size of three animals.

We identified four seasons for home ranges, which we classified by monthly precipitation and temperature (Thompson, 2016). Specifically, we classified January, February, and March as winter/spring, a cold and wet season; April, May, and June as spring/summer, a relatively hot and dry season; July, August, and September as monsoon, a hot and wet season; and October, November, and December as fall/winter, a relatively cold and dry season (Thompson, 2016). We ran Welch’s modified two-sample t-test to compare home range size calculated using MCP vs KDE methods for each animal.


**Habitat-Use Analysis**—We assessed habitat use by gray foxes by comparing proportion of habitat used versus that available on the landscape. We used vegetation layers designated by the U.S. Forest Service (2016) to define vegetation communities (Table 2). Habitat use was defined as any point a fox was located at through VHF/GPS radio collars or visual observations. We examined the number of locations per vegetation community and examined the proportion of locations of each type that was used. Proportion of available habitat was determined as percent area covered by each type within the study area (Marcum and Loftgaarden 1980). We performed chi-square tests to compare habitat use vs availability per individual in each study site.

**RESULTS**—**Home Range**—Three gray foxes had > 70 points from winter/spring of 2016 to spring/summer 2017 from GPS locations and seven gray foxes had ≥ 3 points from winter/spring of 2016 to spring/summer 2017 from VHF locations. We analyzed MCP and KDE home ranges for the three foxes with > 70 points: two males from the White Mountains and one female from the Pinaleño Mountains. Mean home range size (± SD), across all seasons, from MCP was 5.15 km² ± 3.91 and for KDE was 3.78 km² ± 2.74 with a large amount of individual variation. MCP home ranges were larger than kernel density estimates. Maximum distance moved by foxes was calculated over a 7h time period (standard time between GPS fixes) which varied over the 24h day. Across all seasons, maximum distance moved averaged at 2.2 km ± 1.07 (SD), with 4.3 km the largest distance moved by any individual across all seasons.

We collected spatial data opportunistically, which lead us to have different seasons sampled and total number of seasonal home ranges per animal (Table 1). For one male in the White Mountains (M102), we collected enough data for a single season in 2016. For the female from Pinaleño Mountains (F201), we were able to calculate seasonal home ranges for two seasons in 2016. The second male from White Mountains (M106), we were able to calculate seasonal home ranges for three seasons in 2016. The female did have significantly different home ranges across seasons (Table 1). The second male (M106) had similar home ranges across all three seasons (Table 1). We found that on average, males had home ranges that were 69% larger than for the female across all seasons regardless of MCP or KDE methods.

**Habitat Use**—Gray foxes selected for upper evergreen forests in the Pinaleño Mountains and used areas of ponderosa pine, upper evergreen pine-oak mix, and pine-oak-juniper mix (Fig 1). In the White Mountains, gray foxes selected for pine-juniper woodlands and used areas of ponderosa pine, grass forb, Douglas fir, and upper evergreen pine-oak mix (Fig 2). Habitat use by gray foxes in both the Pinaleño Mountains and White Mountains did not differ significantly from what was available on the landscape (MG: $\chi^2 = 12.00$, df = 9, p = 0.21; WM: $\chi^2 = 15.08$, df =15, p = 0.45).

**DISCUSSION**—We found that gray foxes in southeastern Arizona had larger home ranges than elsewhere. Gray foxes had home ranges of 3.78 km² on average (KDE), whereas previous studies estimated smaller home ranges (Chamberlain and Leopold, 2000; Chamberlain and Leopold, 2002; Deuel et al., 2017). Space use of gray foxes has been well documented elsewhere (Trapp and Hallberg, 1975; Chamberlain and Leopold, 2002), however not in the southwestern United States (Hoffmeister, 1986; DeYoung et al., 2009). Our study is one of the first conducted on gray fox spatial ecology in Arizona.

Home ranges of gray foxes are typically similar in size between sexes, which is thought to be from a lack of sexual dimorphism in the species (Sawyer and Fendley, 1990; Chamberlain...
and Leopold, 2002). Chamberlain and Leopold (2000) documented size of home ranges and core areas did not differ between sexes but differed among seasons. We saw a significant difference in the seasonal home ranges of our only female gray fox. We were able to track this female in winter/spring and spring/summer 2016. Gray foxes have been documented to den and whelp pups between February to June (Fritzell and Haroldson, 1982). The decrease in home range we saw in this female occurred during the spring/summer of 2016. This dramatic decrease in home range size could be from pup rearing. However, we did not see any significant change in home range across the three seasons we had data on male gray foxes. Our sample size is too small to be able to draw any meaningful conclusions on the differences between males and females in our study areas. However, we do see that for the two individuals we had multi-seasonal data for, the male had larger home range estimates than the female. Our collars were active from 1000 h to 1600 h, the gray foxes in our study were most likely in their bed sites due to their crepuscular/nocturnal behavior (Fritzell and Haroldson, 1982); we suspect this would have a strong influence on our telemetry results.

Gray fox habitat use is highly variable across the United States (Cypher, 2003) and is greatly dependent on habitat availability and the elevation sampled. In the southwestern United States foxes occupied desert-scrub, chaparral, oak or pinyon-juniper woodlands, and ponderosa pine or Douglas fir (Hoffmeister, 1986). Our results showed that gray foxes selected for pine-juniper woodlands and upper evergreen forests as well as areas of mixed forest types with pinyon-juniper, pine-oak, and Douglas fir. We found that foxes in the White Mountains used a wider variety of vegetation types than individuals in the Pinaleño Mountains, which may have simply been a function of available vegetation types.

Our study was conducted at elevations between 1,800-2,800 m, which is a much higher elevation for gray foxes than in previous studies (Fritzell and Haroldson, 1982; Hoffmeister, 1986; Deuel et al., 2017). This difference in elevation plays a role in what vegetation types were available to these two populations of gray foxes that could account for the differences in what vegetation types were selected in this study (Trapp and Hallberg, 1975; Fritzell and Haroldson, 1982; Hoffmeister, 1986; DeYoung et al., 2009).

Our results suggest that diversity of vegetation types use by gray foxes is related to availability, but that overall space use does not differ in an isolated vs well-connected landscape. Gray foxes are habitat generalists in southeastern Arizona (Fritzell and Haroldson, 1982; Hoffmeister, 1986) and that space use by this species is highly variable based on the availability of vegetation (Crooks, 2002; Cypher, 2003; Aldridge, 2008).

Zoonotic disease transmission dynamics are complex. Pathogen transmission and persistence over space and time can be highly variable due to host species population dynamics (Alexander et al., 2012). Understanding spatial dynamics is a critical component in attempts at predicting the emergence or spread of an infectious disease (Smith et al., 2002). Spatial distribution of hosts and variation in local contact rate are key components for predicting disease spread in heterogeneous landscapes (Smith et al., 2002).

The goal of our study was to examine the spatial distribution of gray foxes as both a host and reservoir species for rabies lyssavirus in Arizona. While our sample sizes were small, we began to understand how gray foxes use space in the state. Gray foxes in our study had highly
variable home range sizes and habitat use in both continuous and isolated forests at high elevations. Our results support that foxes are habitat generalists (Fritzell and Haroldson, 1982; Hoffmeister, 1986). Despite being generalists, we still found areas that gray foxes used more than what was available, such as pine-juniper woodlands in the White Mountains and upper evergreen forests in the Pinaleño Mountains.

Previous research on the control of gray fox rabies in Texas using oral vaccine distribution (ORV), found that at the landscape scale, management units that were defined too conservatively result in wasted effort (DeYoung et al., 2009). This indicates that defining specific vegetation communities and areas of high occupancy by gray foxes, will increase efficiency for ORV. ORV has proven to be a successful method in the past for controlling the spread of gray fox rabies in the southwestern United States (DeYoung et al., 2009; Slate et al., 2009). Other tactics for controlling rabies epizootics in wildlife populations include trapping/vaccination/release, removal, intensive monitoring, and funding of research projects (Rosatte, 2001), all of which can be more efficient when informed by home range and habitat use of the vector species.

Strains of the rabies virus that have become established in mesocarnivore populations in the Americas present serious challenges for the elimination of enzootic rabies in domestic dogs (Canis familiaris) and the subsequent reduction of the rabies burden on humans (Velasco-Villa et al., 2017). There is a continued risk of these strains becoming re-established in dog populations, due to spillovers from wildlife into unvaccinated dogs being common in rural areas (Velasco-Villa et al., 2017). Urban sprawl is projected to increase as human populations grow, indicating that wildlife will come into contact at higher rates with unvaccinated dogs and other domestic animals. The southwestern United States has experienced rapid population growth and urban expansion for the past 150 years and is projected to grow by an additional 19 million people by 2030 (from 2010; Theobald et al., 2013). Disease management for rabies epizootic events in the southwestern U.S. will benefit from our study of gray fox space use as zoonoses stemming from wildlife and human populations increase.

We recommend targeting specific areas for ORV and trapping/vaccination/release programs. In Arizona at high elevations, gray foxes selected for pine-juniper woodlands and upper evergreen forests. Disease management could benefit from selectively targeting areas where these vegetation communities occur, increasing the likelihood that a gray fox will encounter an opportunistically placed vaccine bait. ORV distribution effort and efficacy could be improved by focusing on areas that include vegetation communities selected for by gray foxes.
Thank you to N. Dutt, P. Castillo, A. Sanchez, M. Lawling, J. Carpenter, M. Mazzamuto, M. Zandarski, B. Grube, B. Mayer, K. Miller, C. Shaw, M. Morandini, A. Burnett, L. McHugh, A. La Port, K. Bennett, K. Sheehan, and A. Blair for assistance with field work. Many thanks to M. Merrick for GIS analysis help and V. Greer for assistance with equipment and protocols. Thanks to J. Dolphin, A. Howard, S. Sprague, T. Sprague, R. Herriman, S. Simpson, E. Zylstra, M. Bucci, R. Steidl, and J. Heffelfinger for their help with various aspects of the project. Thank you to I. M. Vela Vargas for translating our work into Spanish for readers. This project would not have been possible without the support of the great people at USDA-APHIS Wildlife Services: V. Burton, C. Carrillo, P. Bracco, J. Schweikert, D. Williams, and R. Chipman. The support and guidance of the members of the Koprowski Conservation Research Lab was invaluable to this project. Work was funded by the USDA-APHIS Wildlife Services, National Wildlife Research Center, and T & E, Inc. with additional support from Arizona Game and Fish Department and the University of Arizona.
LITERATURE CITED


FIGURES

FIGURE 1—Habitat use by gray foxes vs availability in the Pinaleño Mountains, Arizona. Available habitat was classified as a proportion of the study area represented by each type. This proportion was compared to the proportion of spatial points collected from gray foxes per vegetation community. (POJ= Pine-Oak-Juniper Woodlands, PP= Ponderosa Pine, UEF= Upper Evergreen Forest, UPO= Upper Pine-Oak Woodlands).
FIGURE 2—Habitat use by gray foxes vs availability in the White Mountains, Arizona. Available habitat was classified as a proportion of the study area each type covered. This proportion was compared to the proportion of spatial points collected from gray foxes per vegetation community. (AE= Aspen Evergreen Woodlands, DF= Douglas Fir, GO= Gambel Oak, GF= Grass Forb Mix, PJ= Pine Juniper Woodlands, PP= Ponderosa Pine, UEF= Upper Evergreen Forest, UPO= Upper Pine-Oak Woodlands, WF= White Fir).
TABLE 1—Summary of total and seasonal home ranges for individual foxes in the Pinaleño and White Mountains, Arizona. Maximum distance moved over a 7h time interval; GPS points were collected every 7 hours.

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>Study Site</th>
<th>Sex</th>
<th>Season</th>
<th>Method</th>
<th>Area (km²)</th>
<th>Maximum Distance (km)</th>
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</thead>
<tbody>
<tr>
<td>F201</td>
<td>MG</td>
<td>F</td>
<td>WS16</td>
<td>MCP</td>
<td>3.04</td>
<td>1.71</td>
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<td></td>
<td>KDE</td>
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</tr>
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<td>MCP</td>
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<td></td>
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<tr>
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<tr>
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<td>Total</td>
<td>MCP</td>
<td>1.86</td>
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<td>KDE</td>
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</tr>
<tr>
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<td>WM</td>
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<td></td>
<td>M16</td>
<td>MCP</td>
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<td></td>
</tr>
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<td>KDE</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td>MCP</td>
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<td></td>
<td></td>
<td>KDE</td>
<td>6.34</td>
<td>2.05</td>
</tr>
</tbody>
</table>
### Table 2

Definition of vegetation communities present in the Pinaleño and White Mountains, Arizona. Scientific names of tree species classified within each vegetation community.

<table>
<thead>
<tr>
<th>Community Name</th>
<th>Abbreviation</th>
<th>Species Included</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pine-Oak-Juniper</td>
<td>POJ</td>
<td>alligator juniper (<em>Juniperus deppeana</em>), Gambel oak (<em>Quercus gambelii</em>), ponderosa pine (<em>Pinus ponderosa</em>), white pine (<em>Pinus strobiformis</em>)</td>
</tr>
<tr>
<td>Pine-Juniper Woodlands</td>
<td>PJ</td>
<td>alligator juniper (<em>Juniperus deppeana</em>), ponderosa pine (<em>Pinus ponderosa</em>), white pine (<em>Pinus strobiformis</em>)</td>
</tr>
<tr>
<td>Upper Evergreen Forest</td>
<td>UEF</td>
<td>cork-bark fir (<em>Abies lasiocarpa</em> var. <em>arizonica</em>), Douglas fir (<em>Pseudotsuga menziesii</em>), Engelmann spruce (<em>Picea engelmanii</em>), white fir (<em>Abies concolor</em>)</td>
</tr>
</tbody>
</table>
APPENDIX C: Supplemental data on gray fox (*Urocyon cinereoargenteus*) captures, body measurements, and home ranges

The following table contains capture and raw data of home range estimates (95% fixed kernel and minimum convex polygon) for gray foxes in the Pinaleño and White Mountains, Arizona between January 2016-October 2016.
TABLE 1—Total home range size of individual gray foxes calculated using kernel density estimate (95%) or minimum convex polygon (100%) methods in the Pinaleño and White Mountains, Arizona.

<table>
<thead>
<tr>
<th>Animal ID</th>
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<th>Sex</th>
<th>Area (km²)</th>
<th>Number of Points</th>
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<td>M</td>
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<td>72</td>
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<tr>
<td>M106</td>
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<td>WM</td>
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<td>6.34</td>
<td>1633</td>
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<td>Kernel</td>
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<td>663</td>
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<tr>
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<td>MCP</td>
<td>MG</td>
<td>F</td>
<td>3.04</td>
<td>663</td>
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<td>MG</td>
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TABLE 2—Summary of total and seasonal home ranges for individual foxes in the Pinaleño and White Mountains, Arizona. Maximum distance moved over a 7h time interval; GPS points were collected every 7 hours.

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>Study Site</th>
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<th>Season</th>
<th>Method</th>
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TABLE 3—Summary of body measurements for captured gray foxes in the Pinaleño and White Mountains, Arizona. Age is listed as adult (A) and subadult (SA).

<table>
<thead>
<tr>
<th>Date</th>
<th>Study Site</th>
<th>Sex</th>
<th>Age</th>
<th>Animal ID</th>
<th>Mass (kg)</th>
<th>Ear Length (L/R) (cm)</th>
<th>Tail Length (cm)</th>
<th>R Hind Foot Length (cm)</th>
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<td>01/17/16</td>
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<td>A</td>
<td>Unmarked</td>
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<td>---</td>
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<td>01/17/16</td>
<td>WM</td>
<td>M</td>
<td>A</td>
<td>M101</td>
<td>3.5</td>
<td>8.5/7.5</td>
<td>39.0</td>
<td>13.5</td>
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<tr>
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<td>M</td>
<td>A</td>
<td>M102</td>
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<td>7.2/7.9</td>
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