INFLUENCE OF HABITAT HETEROGENEITY AND WATER SOURCES ON KILL SITE LOCATIONS AND PUMA PREY COMPOSITION

BY

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ABSTRACT

Habitat heterogeneity and the availability of man-made water sources influence puma diet composition and the location of kill sites in the arid regions of the southwestern United States. To determine if habitat heterogeneity and corresponding prey diversity influence puma diet composition, puma diet was examined in New Mexico, at sites representing riparian areas adjacent to the Rio Grande and xeric Chihuahuan Desert uplands. We determined seasonal prey composition and describe differences in prey composition between pumas occupying distinct cover types. Prey composition varied, with more ungulate prey being consumed by pumas inhabiting the upland desert areas and more aquatic prey consumed in the riparian bosque. The diverse diets of the pumas inhabiting the heterogeneous habitats in southcentral New Mexico provides additional evidence supporting that pumas have broad diets that are strongly influenced by the habitat and prey community that their home range encompasses. To determine if man-made water sources influence puma habitat use and kill site locations, puma diet data was compiled from seven study areas in the Chihuahuan and Sonoran deserts. The proximities of ungulate kill sites to man-made water sources were compared with point locations generally available within puma home ranges. Mixed effects logistic regression was used to determine if the probability of a site being a kill location was related to the proximity to water sources and or other habitat characteristics. While pumas did not appear to be exploiting the predictable prey visitation of man-made water sources, they were capitalizing on restricted distribution of prey within 5 km of water sources. At the home range scale, puma use areas proximate to water sources that likely have increased prey abundance and higher probabilities of encountering prey for hunting. Within their home ranges, pumas also select fine scale habitat features, such as woody cover, that enhance their ability to stalk, ambush, and effectively kill prey.

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CHAPTER 1

Habitat Heterogeneity in the Chihuahuan Desert and Puma Diet Diversity

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ABSTRACT

Several studies describe puma diets in the arid regions of the southwestern United States within homogenously xeric locations, overlooking the influence of landscape diversity generated by riparian forests. Such habitat heterogeneity and corresponding prey diversity could influence puma habitat use, prey availability and diet composition. Therefore, we examined puma diet in New Mexico, at sites representing riparian areas adjacent to the Rio Grande and xeric Chihuahuan Desert uplands. We determined seasonal prey composition and describe differences in prey composition between pumas occupying distinct cover types. We collected prey composition data from 686 kill sites made by GPS-collared pumas on the Armendaris Ranch and Sevilleta National Wildlife Refuge from 2014 to 2018. Diet composition included 32 different avian, aquatic, small mammal and ungulate prey species. Prey composition varied, with more ungulate prey being consumed by pumas inhabiting the upland desert areas and more aquatic prey consumed in the riparian bosque. Prey composition differed between seasons, with ungulate prey decreasing and aquatic prey increasing during the hot-dry season. Diet varied between puma sex and habitat affinity with females in the desert uplands consuming more small mammals than either males or females in riparian areas. The diverse diets of the pumas inhabiting the heterogeneous habitats in southcentral New Mexico provides additional evidence supporting that pumas have broad diets that are strongly influenced by the habitat and prey community that their home range encompasses.

INTRODUCTION

Puma (*Puma concolor*) are a widely distributed predator, occupying areas from the Andean Mountains in southern Argentina to the Yukon and Northwestern Territories in northern Canada (Currier 1983; Mulders et al. 2001; Jung et al. 2005; Elbroch et al. 2014). Across their distribution range, pumas inhabit areas with diverse environmental conditions ranging from the marshy Florida Everglades (Maehr et al. 2002), densely vegetated neotropical forests (Novack et al. 2005), and the xeric deserts in North and South America (Franklin et al 1999; Logan and Sweanor 2001; Choate et al. 2018). The generalized dietary habits and extreme mobility allow puma to thrive in widely varying environmental conditions and utilize an array of species as prey.

Pumas prey opportunistically on the most abundant and vulnerable species across their distribution range (Anderson 1983; Logan and Sweanor 2001). For example, puma consume a variety of prey species ranging in size from beetles (*Chrysomelidae* spp., Cashman et al. 1992) and rodents (Cunningham et al. 1999) in Arizona, to feral horses (*Equus caballus*) and moose (*Alces alces*, Knopff et al. 2009; Bacon et al. 2011) in Alberta, Canada. In South America, puma prey upon guanaco (*Lama guanicoe*), vicuna, (*vicugna vicugna*), European hare (*Lepus europaeus*), lesser rhea (*Pterocnemia pennata*), tapir (*Tapirus terrestris*), and pudu (*Pudu pudu*, Iriarte et al. 1991; Franklin et al. 1999; Hernandez-Guzman et al. 2011; Azevedo et al. 2016; Gelin et al. 2017). In Central America, puma prey on white-tailed deer (*Odocoileus virginianus*), collared peccary (*Pecari tajacu*), coatimundi (*Nasua narica*), nine-banded armadillo (*Dasypus novemcinctus*), and various lagomorph species (*Lepus* spp., *Sylvilagus audubonii*; Nunez et al. 2000; De La Torre et al. 2009). Pumas in North America frequently prey upon large ungulates such as deer (*Odocoileus* spp.), elk (*Cervus canadensis*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*), as well as a variety of smaller mammals such as beaver (*Castor canadensis*), coyote (*Canis latrans*), raccoon (*Procyon lotor*), and skunk (*Mephitidae* spp.). Livestock, including cattle (*Bos tarus*), sheep (*Ovis aries*), and goats (*Capra aegagrus*), are also commonly depredated by puma throughout the Americas in areas with ranching and agriculture (Rominger et al. 2004; Polisar et al. 2003). Although puma diet composition can be extremely diverse, many studies have reported deer to be the preferred prey resource utilized by pumas across many of the different ecoregions (Iriarte et al. 1990; Logan and Sweanor 2001; De La Torre et al. 2009; Villepique et al. 2011). In many cases, deer comprise more than 50% of the prey items documented in puma diets in previous studies (Logan and Sweanor 2001; Wilkens et al. 2015).

Prey availability and vulnerability are influenced by habitat conditions (Luttbeg et al. 2003). Areas with heterogeneous habitat conditions have increased prey and vegetation diversity compared to more homogeneous structured habitats (Kerr. et al. 1997). This diversity in heterogeneous landscapes affects habitat use and diet for both predators and prey (Hebblewhite et al. 2005). Prey often benefit from habitat heterogeneity because the increased diversity in forage can enhance their ability to meet their nutritional and energetic demands compared to homogenous habitats. Prey can also reduce predation risk in heterogeneous habitats by selecting areas with dense vegetation to evade cursorial predators (e.g., wolves) or less vegetated areas with higher visibility to evade ambush predators (e.g., puma). Predators can benefit from habitat heterogeneity because of the increased diversity and abundance of prey. The generalist diets and adaptability to various environmental conditions allow pumas to exploit the diversity of prey and habitat conditions within heterogeneous landscapes (Tattersall et al. 2002). This is especially true in areas where habitat heterogeneity increases the amount stalking cover and enhances the ability of pumas to ambush prey.

There have been several puma diet studies in the arid regions of the southwestern united states, most of which occurred in areas where the landscape is homogenously xeric desert (Cunningham et al. 1999; Logan and Sweanor 2001; Choate et al. 2018). However, the landscape in south-central New Mexico consists of xeric upland desert areas bisected by the riparian bosque habitat bordering the Rio Grande. This heterogeneity in vegetation should result in increased prey diversity and can potentially influence puma habitat use and diet composition. To assess the relationship between habitat heterogeneity and puma diet composition, I conducted a four-year study (2014 – 2018) to examine puma diet through field investigation of GPS clusters at two desert study areas adjacent to the Rio Grande in south-central New Mexico. My specific objectives were to determine seasonal variation in prey composition and describe differences in prey composition of pumas occupying the two diverse habitats including the mesic riparian bosque along the Rio Grande and xeric Chihuahuan Desert upland habitat.

STUDY AREA

I conducted this study on the Armendaris Ranch (AR) and Sevilleta National Wildlife Refuge (SNWR) in south-central New Mexico (Fig. 1). The Armendaris Ranch located 24 km east of Truth or Consequences, New Mexico, is a 146,854 ha private bison (*Bison bison*) ranch. The AR is bordered by the San Andres Mountains on White Sands Missile Range (WSMR) to the east, the Bosque del Apache National Wildlife Refuge to the north, the Rio Grande river and Elephant Butte Reservoir to the west. Elevation ranges from 1,340 m along the Rio Grande to 2,083 m in the Fra Cristobal Mountains. Vegetation types on the AR are comprised mostly of Chihuahuan desert scrub and desert grasslands with sparse pinyon-juniper (*Pinus edulis,* *Juniperus* spp.) woodlands at higher elevations in the Fra Cristobal Mountains. The landscape is primarily xeric desert, except for the lush strip of riparian bosque bordering the Rio Grande and edges of Elephant Butte Reservoir. Common plant species in the desert upland areas include creosote bush (*Larrea tridentata*), fourwing saltbush (*Atriplex canescens*), ocotillo (*Fouquieria splendens*), longleaf ephedra (*Ephedra trifurca*), gramma grasses (*Bouteloua* spp.), juniper (*Juniperus deppeana, J. monosperma*), prickly pear (*Opuntia* spp.) and cholla cacti (*Cylindropuntia* spp.). Whereas common plant species in the Rio Grande riparian bosque include salt cedar (*Tamarix ramosissima*), Russian olive (*Elaeagnus angustifolia*), cottonwood (*Populus wislizeni*), kochia (*Kochia scoparia*), and willow (*Chilopsis linearis, Salix exigua*). Mean annual precipitation is 23. 7 cm (SD ± 7.6) and mean annual snowfall is 8.6 cm (SD ± 15.5). Temperatures range from an average daily minimum of 5.3°C (SD ± 3.1) in January to an average daily maximum 30.6°C (SD ± 2.3) in July (climate data from Elephant Butte Dam, Truth or Consequences, NM; WRCC 2018a).

Ungulates common in the xeric uplands on the AR include mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), non-native gemsbok (*Oryx gazella*), collared peccary (*Pecari tajacu*) and desert bighorn sheep (*Ovis canadensis mexicana*) in the Fra Cristobal Mountains. Potential prey species inhabiting the riparian areas adjacent to the Rio Grande include beaver (*Castor canadensis*), raccoon (*Procyon lotor*), Rio Grande wild turkey (*Meleagris gallopavo intermedia*), and various aquatic species such as spiny softshell turtle (*Apalone spinifera*), and common carp (*Cyprinus carpio*). Other predators on the AR include coyote (*Canis latrans*), bobcat (*Lynx rufus*), grey fox (*Urocyon cinereoargenteus*), golden eagle (*Aquila chrysaetos*), and transient black bears (*Ursus americanus*). The riparian bosque bordering Elephant Butte Reservoir and the Rio Grande also provide an important wintering area for migratory waterfowl. The availability of waterfowl as potential prey dramatically increases during the winter (Kelly et al. 1999).

The SNWR, located 30 km north of Socorro, New Mexico, is a 93,077 ha wildlife refuge managed by U.S. Fish and Wildlife Service. The SNWR is approximately 75 km north of the Armendaris Ranch (Fig. 1). The landscape at the SNWR is comparable to the AR and is comprised of xeric upland desert areas and riparian bosque bordering the Rio Grande. Elevation ranges from 1,432 m along the Rio Grande to 2,529 m in the Pino and Ladrone mountain ranges. The xeric upland areas consist of Chihuahuan desert scrub, Great Plains Short Grass Prairie, Colorado Plateau Shrub Steppe at lower elevations and pinyon-juniper woodland in the Pino and Ladrone mountains. The vegetation within the Rio Grande riparian bosque is nearly identical to the AR, but also has some restored wetland and waterfowl management areas. The vegetative characteristics of the SNWR are similar to the AR, but with more pinyon pine, oak (*Quercus grisea, Q. gambelii*), and juniper in the higher elevations. The temperatures range from an average daily minimum of 2.1°C (SD ± 4.3) in January to an average daily high of 25.2°C (SD ± 2.6) in July. Mean annual rainfall is 20.6 cm (SD ± 6.6), with mean annual snowfall of 11.8 cm (SD ± 12.2; climate data from Bernardo, NM: WRCC 2018b).

Common mammals in the upland desert areas at the SNWR include elk (*Cervus canadensis*), aoudad (*Ammotragus lervia*), Rocky Mountain bighorn sheep (*Ovis canadensis*), and desert bighorn sheep at higher elevations and feral horses (*Equus caballus*), pronghorn, mule deer, and gemsbok at lower elevations. Common predators include coyote, bobcat, gray fox, and resident populations of black bear. Public access to the SNWR is restricted, however some waterfowl and upland gamebird hunting is permitted. Both study areas border private and public lands (i.e., state trust lands, Bureau of Reclamation, and Bureau of Land Management), most of which are used for livestock ranching, hunting, and agriculture.

Based on long-term climate data, I classified seasons at both study areas as: the cool-dry (CD, November – March), hot-dry (HD, April – June), and hot-wet (HW, July – October) seasons.

METHODS

Capture and Monitoring

I primarily used Aldrich and Fremont foot snares to capture pumas from January 2014 to June 2018 on the AR, and from November 2015 to April 2017 on the SNWR. I monitored snare sets using cellular cameras (Verizon Blackhawk, Covert Scouting Cameras, Lewisburg, KY) and I used VHF trap-site transmitters (TBT-503-3, Telonics Inc., Mesa AZ) to monitor snares in areas lacking cellular service. I programmed the cellular cameras to send a SMS picture message alert immediately upon activity at the snare and I tested cameras for functionality by sending a remote command to the cameras to send a real-time image of snare sites daily at 0700 and 1800 (MST). When using VHF trap-site transmitters, I checked the VHF signal every 6-12 hours, depending on the weather conditions. I checked snare transmitters more frequently during periods with extremely hot (above 32°C) and cold (below 0°C) ambient temperatures. Monitoring snares with VHF transmitters was labor intensive compared to using cellular cameras and limited the total number of snares that I could maintain. Because of this, I typically only used VHF transmitters for situations in which a capture seemed imminent (i.e., fresh puma kill, evidence of recent activity) in areas that did not have cellular service. I also used hounds to capture pumas in areas that provided suitable hunting conditions for hounds and safe escape structures (trees or boulders) for lions. I mostly used hounds to recapture pumas to exchange collars with low battery or those that were malfunctioning. Upon capture, I immobilized pumas using 5 mg/kg ketamine combined with 0.08 mg/kg medetomidine. I used 0.3 mg/kg atipamezole as the antagonist for medetomidine (Kreeger et al. 2002). I used 1-2 ml Pneu Dart Type P Slo-Inject darts fired from a Pneu Dart Excalibur projector (Pneu Dart, Williamsport, PA) to deliver the immobilization drugs. During processing, I recorded the age, sex, and weight for each captured animal. I estimated the age using tooth wear and pelage patterns (Shaw 1986). I collared pumas older than 10 – 12 months with an ATS G2110E GPS-Iridium collar (Advanced Telemetry Systems, Isanti, MN). I marked captured pumas with a visual identification pattern (i.e., reflective color, letter, or number) attached to the collar and ear tagged each puma with a numbered New Mexico Department of Game and Fish tag. In most cases, I was able to limit capture processing and handling times to 60 minutes or less. I closely monitored all captured pumas for complications during capture and post-release. All capture and handling procedures follow acceptable methods (Sikes et al. 2016) and were approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocol 2015-015).

I programmed the collars deployed on the AR to collect 16 GPS fixes per day; hourly intervals during crepuscular and nocturnal periods when pumas are characteristically more active (i.e., 1900 – 0700) and then at three hour intervals during the daytime (i.e., 1000, 1300, and 1600) when pumas are less active. I programmed the collars on the SNWR to collect 8 GPS fixes per day at 3 hour intervals. The GPS data was transmitted via the Iridium satellite system every 12 hours (i.e., 0600, 1800 MST).

Prey Composition Data Collection

I used GPS clusters to identify potential kill sites to determine diet composition. At the AR, I defined a cluster, or potential kill and feeding location, as ≥ 6 consecutive crepuscular or nocturnal locations within a 50-m radius, whereas on the SNWR, to account for the 3-hr fix interval, I defined a cluster as ≥ 2 consecutive crepuscular or nocturnal locations within a 50-m radius. Thus, any location where a puma spent six consecutive crepuscular or nocturnal hours within a 50-m radius was considered a cluster and subject to field inspection. I used AnimalClusters.R (version 1.1) developed by Daniel and Kindschuh (2016) and program R (version 3.1.2; R Core Team 2015) to identify GPS clusters. I then investigated clusters in the field as soon as possible to prevent loss of kill evidence and site data caused by scavengers and weathering; I generally visited all clusters within 14 days of the cluster start date. I located clusters in the field by navigating to the centermost GPS fix within the defined cluster and then outwardly searched the surrounding area within 50 m of each GPS location in the cluster in a spiral-like fashion. I carefully examined each location in the cluster for evidence of a kill (i.e., carcass remains, hair, bone fragments, blood, drag marks, disturbed vegetation and soil; Shaw 1986). Based on the characteristics of the cluster site, I classified each site as a kill site for sites that contained evidence of a kill, bed site for locations that showed sign of the puma being bedded, scat site, hunting location for locations in which the puma appeared to have hidden in cover near a potential ambush location (i.e., game trail, squeeze or area that funneled prey movement), water site for locations containing a water source but no other evidence of use, scavenge site for locations where the puma scavenged an already dead carcass, or unknown for locations that lacked sufficient evidence indicating how the site was utilized.

At each kill site, I used tooth wear, pelage patterns, and the morphological characteristics of the carcass to estimate the age class of prey kills. For ungulate prey, I classified ages as neonate (<1 year), yearling (1-2 years), sub-adult (2-4 years), adult (4-6 years), mature (older than 6 years), and unidentified for prey kills that lacked evidence of age. For non-ungulate prey, I classified age as neonate (younger than 1 year), adult (older than 1 year), and undefined. I used genitalia or secondary sexual characteristics to identify prey sex when possible. I determined if the prey item had been killed by a puma or scavenged by examining the carcass and site for evidence of puma predation (i.e., bite marks to the neck or throat, carcass cache, subcutaneous hematomas on neck or throat, tracks near carcass (Shaw 1986). I also used the rate of decomposition of the carcass relative to the GPS telemetry fix times and dates of the locations at the carcass site. I inspected the carcass remains for signs of malady, injury, deformity, or anything that could have increased its susceptibility to puma predation.

ANALYSES

The riparian bosque bounding both sides of the Rio Grande bisecting the AR and SNWR study areas, and results in diverse habitat conditions and increased diversity of potential prey species for pumas (Figs. 1-2). Aquatic species and some of the small mammal prey species (e.g., raccoon) within the riparian bosque habitat would not have been available prey for pumas had the habitat been homogenously comprised of arid desert. At both study areas, some pumas remained in the riparian bosque habitat, others exclusively used xeric upland areas, and some utilized both areas, regularly moving between riparian bosque and xeric uplands. To account for variation in composition of available prey species related to the predominant use of one vegetation cover type over others, I used satellite imagery in ArcGIS 10.6 (ESRI 2018: 10.6. Redlands, CA) to digitize the boundary between the riparian bosque vegetation along the Rio Grande and the xeric uplands (Figs. 1-2). I then classified each puma as being riparian, upland, or mixed based upon the proportion of their total GPS fixes within the upland and riparian areas: pumas with more than 75% of their cumulative fixes within the riparian area were classified as riparian, pumas with more than 75% of their cumulative fixes in the upland areas were classified as upland, and pumas with less than 75% of their cumulative fixes in either riparian or upland areas were classified as mixed.

Due to the diversity of the potential prey occurring between habitat types, I categorized prey species into four prey classes: avian, aquatic, small mammal, and ungulate prey. I then calculated the proportion of kills in each prey class for individual pumas within each season and year. I then used the logit transformation on the proportional data prior to analysis. I used multivariate analysis of variance (MANOVA) to examine differences in the proportion of each prey type by puma sex, predominant habitat type (i.e., riparian, upland, mixed) and season (i.e., cool-dry, hot-dry, and hot-wet). I then used Turkey's HSD post hoc analysis to further assess differences in prey class composition between seasons and puma habitat types. Due to low sample sizes, I conducted all analyses with $\alpha = 0.1$ to reduce the chance of committing a Type II error. All statistical analyses were conducted using SPSS (IBM Corp. Released 2017. IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY: IBM Corp)

RESULTS

I captured 7 male and 4 female puma on the AR from February 2014 through June 2018 and 1 male and 4 female puma on the SNWR from November 2015 through December 2017 (Table 1); data was also collected from one male puma (LM7) that was originally captured by another researcher on the Ladder Ranch near Hillsboro, New Mexico, but dispersed to the AR shortly after capture. I classified 3 males and 4 females as being upland pumas, 2 males and 4 females as riparian pumas, and 4 males as mixed pumas (Table 1). I monitored the pumas for 5,582 total telemetry days (*n* = 17 pumas, mean = 328 days/puma ± 226 days [SD]; Table 1). Female pumas were generally monitored for a longer period (3,442 total days, mean = 430 days/female ± 200 days [SD]) than males (2,140 total days, mean = 237 days/male ± 217 [SD]).

Pumas were monitored for 2,457 telemetry days during the cool-dry seasons, 1,195 telemetry days during the hot-dry seasons, and 1,930 telemetry days during the hot-wet seasons.
I investigated 1,073 cluster locations, of which 686 (64%) were kills or feeding sites. The remaining 387 cluster locations I investigated were classified as bed sites (*n* = 247, 23%), scat sites (*n* = 13, 0.01%), hunting sites (*n* = 45, 4%), scavenge sites (*n* = 2, 0.002%), water locations (*n* = 3, 0.003%), or unknown (*n* = 77, 7%). I found 531 kills on the AR (77%) and 155 kills at SNWR (23%). Female pumas killed 403 prey animals (59% of total kills) and 283 were killed by males (41% of total kills).

I documented 32 different prey species at kill sites ranging from small aquatic prey (e.g., common carp, waterfowl), to large ungulates (e.g., gemsbok, mule deer; Table 2). Mule deer were the most commonly killed prey species (*n* = 195, 28%), followed by coyote (*n* = 84, 12%), beaver (*n* = 70, 10%), raccoon (*n* = 51, 0.07%), carp (*n* = 49, 0.07%), and gemsbok (*n* = 35, 0.05%). Bighorn rams (*n* = 12, 44%) and lambs (*n* = 10, 37%) were killed more than ewes (*n* = 5, 19%); upland, riparian and mixed puma all killed bighorn sheep. Prey composition included 39 kills of avian species (0.06%), 158 kills of aquatic species (23%), 192 kills of small mammal species (28%), and 318 kills of ungulate species (46%; Table 2). I was unable to identify the age and or sex of many of the small mammals, ungulate neonates, and some of the aquatic prey because pumas would consume nearly the entire carcass, leaving only hair, hooves, scales, or some larger bone fragments. For the carcasses that I was able to collect age information, there were 55 neonates (8%), 46 yearlings (7%), 68 sub-adults (10%), 275 adults (40%), 28 mature animals (4%); and 214 kills where there were insufficient remains to adequately estimate the age of the prey kill (31%). I was able to identify the sex for 76 male (11%) and 55 female (8%) prey, most of which were adult ungulates (*n* = 118, 90%); with there being 555 kills (81%) that lacked genitalia or secondary sexual characteristic to determine the sex. I documented 305 kills during the cool-dry season (44%), 101 kills during the hot-dry season (15%), and 280 kills during the hot-wet season (41%).

Mule deer were the most common prey species during the hot-wet ($n = 110$, 39%) and cool-dry ($n = 74$, 24%) seasons, but were the fourth most common species at kill sites ($n = 11$, 11%) during the hot-dry season behind carp, beaver, and coyote. Coyote were the second most common prey species during the cool-dry and hot-wet seasons ($n = 48$, 16% and $n = 21$, 11%) and the third species during the hot-dry season ($n = 13$, 13%). Beaver were common during all three seasons (cool-dry $n = 34$, 11%; hot-dry $n = 14$, 14%; hot-wet $n = 22$, 8%). Carp were the most commonly killed prey species during the hot-dry season ($n = 22$) and comprised 22% of all kills during the hot-dry season. The proportion of raccoons at kill sites was higher during the cool-dry season ($n = 35$, 11%), compared to hot-dry ($n = 3$, 3%) and hot-wet ($n = 13$, 5%) seasons. There were also more waterfowl kills during the cool-dry season ($n = 11$, 4%), compared to the hot-dry ($n = 3$, 3%) and hot-wet ($n = 7$, 3%) seasons.

Prey composition differed between puma habitat classifications for all prey types (aquatic, $F_{2,51} = 22.3$, $P < 0.001$; avian, $F_{2,51} = 5.24$, $P = 0.01$; small mammal, $F_{2,51} = 2.75$, $P = 0.077$; ungulate, $F_{2,51} = 4.05$, $P = 0.026$). Kill sites for pumas predominantly occupying the riparian corridor consisted of 4 times as many aquatic prey than mixed pumas and more than 10 times higher than upland pumas. Riparian pumas also consumed 2-4 times as many avian prey than both mixed and upland pumas (Fig. 3). Kill sites from upland pumas were comprised of 2-3 times as many ungulates as riparian and mixed pumas using both areas (Fig. 3). Small mammal prey were more prevalent at the kill sites of upland (21 total, mean proportion = 0.22 [SD] ±

0.25) and riparian pumas (18 total, mean proportion = 0.25 [SD] ± 0.27) compared to mixed pumas that used both areas (12 total, mean proportion = 0.06 [SD] ± 0.17; Figure 3).

For all puma types, the proportion of kills sites that were ungulates also differed by season ($F_{2,51} = 2.61$, $P = 0.087$). Ungulate prey were 3-4 times more common at kill sites during the cool-dry and hot-wet seasons than during the hot-dry season (Figure 4). The proportion of kills composed of small mammal prey differed by puma habitat classes and puma sex (puma habitat class × puma sex interaction; $F_{1,52} = 3.32$, $P = 0.077$, Fig. 5). Upland female pumas consumed the highest proportion of small mammal prey, 2-3 times as many as did upland, riparian and mixed males; and approximately 6% more than riparian females. Proportion of kill sites composed of avian prey were dependent on puma habitat class, season, and sex (puma habitat class × season × sex interaction, $F_{6,23} = 2.62$, $P = 0.087$) with upland female pumas having a higher proportion of avian prey during the hot-dry season. However, this interaction was likely influenced by one upland female (ARF03) who became extremely emaciated likely due to a large concentration of intestinal worms and began ambushing low-lying bird nests just prior to her death.

Ungulate prey had the highest mean proportion of the combined diet across all three seasons with the highest during the hot-wet season (0.524 ± 0.374 [SD]). There were more aquatic prey killed during the hot-dry season ($n = 40$ aquatic prey, $n = 31$ ungulate prey), however the mean proportion of ungulates (0.2348 [SD] ± 0.32768) in the combined diet was still higher than that for aquatic prey (0.1890 [SD] ± 0.3612). Smaller mammal prey had the second highest mean proportion during the cool-dry (0.2386 [SD] ± 0.23455) and hot-wet (0.1549 [SD] ± 0.1690) seasons, but had a slightly lower mean proportion than aquatic prey during the hot-dry season (0.1829 [SD] ± 0.31077). Avian prey represented the lowest mean proportion of the diet across all three seasons with the highest proportion during the hot-dry season (0.0405 [SD] ± 0.12686) and lowest during the hot-wet season (0.0115 [SD] ± 0.03810; Figure 4).

DISCUSSION

Puma diet diversity found in this study was mostly due to the extreme diversity in habitat conditions and prey availability between the mesic riparian bosque along the Rio Grande and surrounding xeric Chihuahuan desert. The diet breadth documented in many previous puma diet studies is often less than 20 different prey species. Approximately 15 different species were consumed by jaguars and pumas in Sonora, Mexico (Rosas-Rosas et al. 2008), 17 different species in northeast Oregon (Clark et al. 2014), 13 species in the badlands of North Dakota (Wilkens et al. 2015), 15 species in the Maya Biosphere Reserve, Guatemala (Novak et al. 2005), and 10 species in Banff National Park, Canada (Knopff et al. 2010). Harveson et. al (2000) reported pumas utilizing 10 different prey species in a heterogeneous south Texas landscape that was comprised of 42% riparian and 58% upland habitat. However, Elbroch et al. (2019) reported pumas consuming more than 40 different species in the heterogeneous Greater Yellowstone Ecosystem, Wyoming. Most previous puma diet studies in desert areas occurred in areas that lacked wetland habitat and had little or no aquatic prey available (Logan and Sweanor 2001; Choate et al. 2018). Seven of the 32 prey species (22%) that we documented did not occur outside of the riparian bosque and would not have been included in the diet had the landscape been homogenously desert.

Although I documented more prey species being consumed than many previous desert diet studies, my results are still similar to previous studies in that large ungulates, primarily deer, are the preferred prey of pumas (Logan and Sweanor 2001; De La Torre et al. 2009; Villepique et al. 2011; Wilkens et al. 2015). The prey composition of pumas restricted to the upland areas strongly suggests that had the landscape been homogenously arid desert without the riparian bosque, my results would have closely resembled the ungulate dominated diets documented by Logan and Sweanor (2001) in the nearby San Andres Mountains (i.e., ungulates, primarily mule deer, composed 92% of the diet). The diets of the upland pumas in this study consisted of 70% ungulate prey, 28% small mammal prey, and 2% aquatic and avian prey. However, the diet composition of riparian pumas was more similar to those within South American neotropical areas where puma diet is mostly comprised of smaller prey items due to the increased abundance of small prey species (Iriarte et al. 1990; Monroy-Vilchis et al. 2009; Gomez-Ortiz et al. 2011). The diets of riparian pumas in this study consisted of only 26% ungulate prey and 74% aquatic, small mammal, and avian prey. Beaver were an essential resource for riparian pumas and comprised 42% of the 158 aquatic species kills. Only four male pumas were classified as mixed habitat users and their diet was more similar to that of the upland pumas with 62% ungulate prey, 38% small mammal and aquatic prey. Female pumas were more selective of habitat type, spending 90% to 100% of their time within their chosen habitat but were less selective of prey class and utilized all prey classes. Whereas males utilized both habitats more generally, spending 53% to 96% of their time within their chosen habitat but were more selective of prey class than females.

Elk kills were uncommon and only comprised 2% of the total kills documented. Elk occurred at lower densities in my study areas and were generally located in agricultural or wetland areas near the Rio Grande (i.e., Bosque del Apache NWR, agricultural areas near Socorro, NM) and at higher elevations on the SNWR, which likely limited their availability as potential prey for the majority of pumas in my study. Gemsbok, an elk-size non-native ungulate, occurred at higher densities (Bender et al. 2019) and were frequently preyed upon by male; 3 males killed 89% of gemsbok and infrequently by female pumas (2 females killed 3 gemsbok). Predation of adult gemsbok was unexpected, as only three neonate gemsbok kills were documented by Logan and Sweanor (2001) between 1985 and 1995 in the nearby San Andres Mountains. Gemsbok evolved with African lion (*Panthera leo*) predation in the arid regions of southern Africa. As a result of which, gemsbok have thicker skin and muscular tissue in their neck protecting their spine and spear-like horns averaging 60-150 cm in length as weaponry to defend against predators (Logan and Sweanor 2001; Edgington 2009). Many of the gemsbok kills that I documented were neonates, however one mature male puma killed 29 adult gemsbok on WSMR which comprised 58% (n = 29) of his total kills. Bighorn sheep only represented 8% (n = 27) of the ungulate kills. However, the low contribution of bighorn sheep to the kill composition was almost certainly influenced by an active management program that included the lethal removal of pumas who killed multiple (5) bighorn sheep in the Fra Cristobal and Ladrone mountains. Bighorn sheep were preyed upon throughout the year, with a slight increase during lambing season from February through May. All but one of the bighorn sheep kills were made by male pumas in the Fra Cristobal and Caballo mountains, the exception being one ram killed by a female puma in the Pino Mountains on the SNWR. Although, pumas regularly utilized areas with livestock, mostly cattle, I only documented a few instances of livestock predation and most were beef calves, but I did document one feral goat killed in the bosque along the Rio Grande.

The proportion of ungulate prey being highest during the hot-wet season is probably caused by the increased availability of mule deer fawns during fawning season (July through September). Fawns and yearlings comprised 55% (n = 60) of the mule deer kills and 21% of the total kills during the hot-wet season. The percent of fawn kills documented during the hot-wet season is consistent with the findings of Logan and Sweanor (2001) on WSMR and also the findings of Kay (2018) in the neighboring Gallinas Mountains near Corona, New Mexico. The increase in aquatic prey consumption during the hot-dry season coincides with the carp spawning season, during which carp are more susceptible to puma predation as they use shallower waters (1 to 4 feet in depth) to spawn. Typically, the carp were caught out of the Rio Grande in shallower water in areas where the riverbank was flat and provided ambush cover (i.e., vegetation, driftwood snags) for pumas. There were a few instances in which carp became trapped as flooded areas adjacent to the Rio Grande dried allowing pumas to easily kill and sometimes scavenge newly dead carp. One young female lion (ARF02) seemed to specialize (Elbroch et al. 2013) in killing turtles as she was responsible for 15 (94%) of the spiny-softshell turtle kills. The majority of the spiny-softshell turtle kills occurred during August-September which is typically when the flooded areas adjacent to the Rio Grande become dry, forcing the turtles to travel back to the Rio Grande. August is also when female turtles lay their eggs in nests burrowed in dry sandy areas, this may have also increased their vulnerability to puma predation (Stebbins 2003). Although the availability of waterfowl increases considerably during the cool-dry season, there was only a slight increase in waterfowl kills compared to other seasons.

The shortened nighttime GPS fix interval and promptness in field investigation of cluster sites improved my ability to locate prey kills, especially those with smaller prey species (Knopff et al. 2009). I found that very small prey items such as lagomorphs and rodents were difficult to detect using GPS cluster investigation and are therefore likely to be underrepresented in my data (Bacon et al. 2011). For the rabbit kills that I was able to locate, typically only feet, ears (jackrabbit), or a few tufts of fur remained as evidence (Elbroch et al. 2013). The small aquatic prey kills were easier to locate due to more carcass remnants as pumas did not eat feathers (waterfowl), shells (turtles), or scales and gill plates (carp). I was unable to investigate the clusters that occurred on private lands outside of my study areas and White Sands Missile Range as promptly due to access restrictions. The delay may have reduced my ability to detect smaller non-ungulate prey at those sites.

CONCLUSION

The diverse diets of the pumas inhabiting the heterogeneous habitats in southcentral New Mexico provides additional evidence that pumas are predators that utilize a multitude of prey species and are capable of inhabiting extremely diverse habitats. Pumas have broad diets that are strongly influenced by the habitat and prey community that their home range encompasses. Additionally, puma diet is likely to be more diversified in areas with heterogenous habitat conditions that support a wider variety of prey species. This is especially true in desert systems where habitat conditions typically do not support higher densities of ungulate prey and pumas are forced to exploit a variety of smaller species to maintain fitness between ungulate kills.

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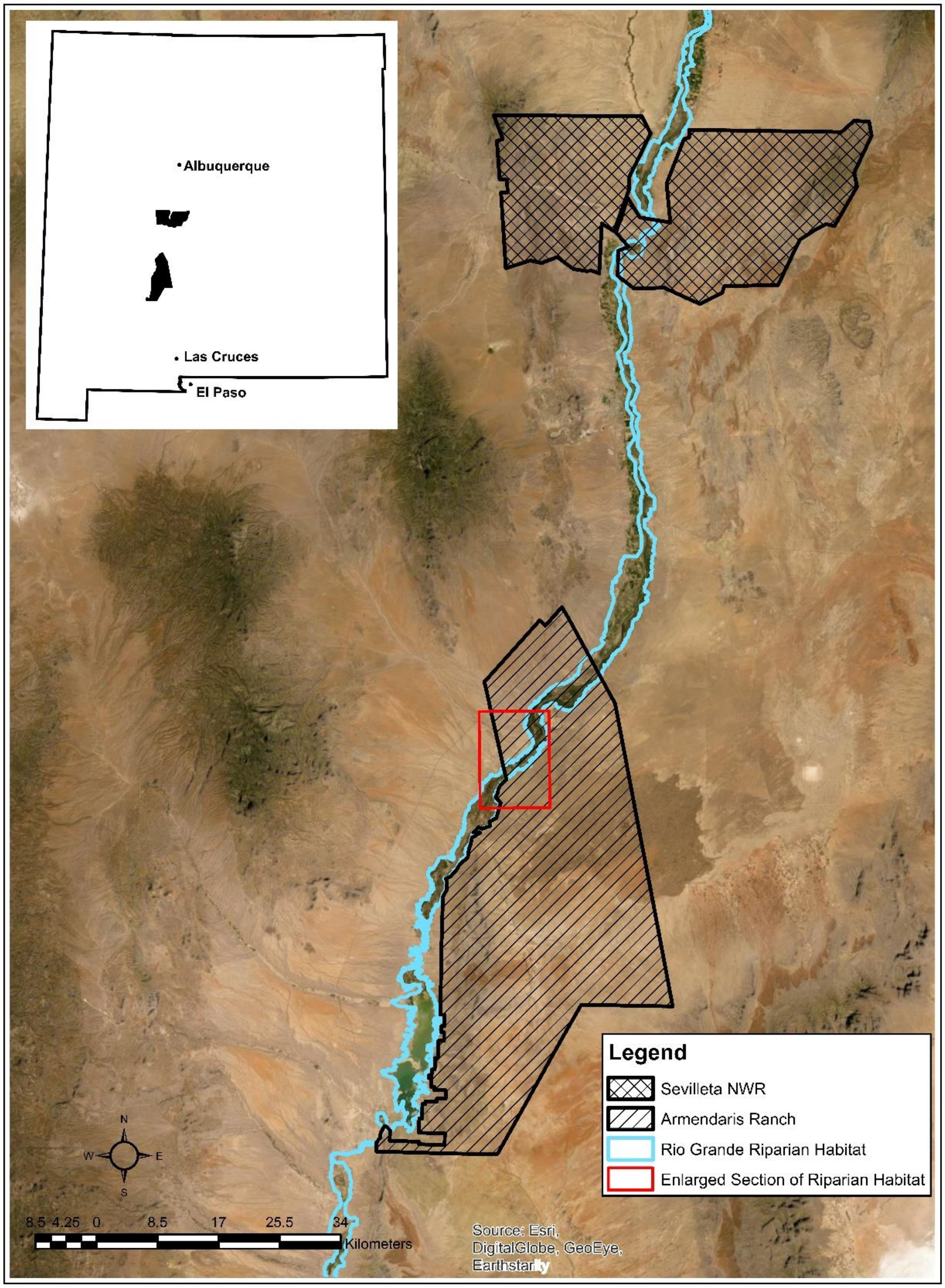
Table 1: Puma sex, age, monitoring period, collected data, habitat classification, and prey class proportions for satellite collared pumas captured on the Armendaris Ranch and Sevilleta National Wildlife Refuge in south-central New Mexico, from 2014 – 2018. Puma habitat classification based upon the proportion of fixes within habitat type; riparian bosque or upland desert. Proportion of kills per prey class for each individual puma were calculated using logit transformed data.

Puma ID	Puma Sex	Puma Age (years)	No. of Days Monitored	No. GPS Fixes Collected	No. Kills Documented	Proportion of GPS Fixes in Upland Habitat	Proportion of GPS Fixes in Riparian Habitat	Puma Classification	Proportion of Kills per Prey Class			
									Aquatic	Avian	Small Mammal	Ungulate
ARF01	Female	4 - 6	712	8668	81	3%	97%	Riparian	48%	1%	23%	27%
ARF02	Female	2	183	2550	48	2%	98%	Riparian	83%	4%	8%	4%
ARF03	Female	4 - 5	326	4468	57	100%	0%	Upland	0%	5%	49%	46%
ARF05	Female	1 - 2	530	7000	65	8%	92%	Riparian	15%	6%	63%	15%
ARM01	Male	6	144	1874	19	57%	43%	Mixed	0%	0%	16%	84%
ARM04	Male	4	53	768	12	56%	44%	Mixed	33%	0%	58%	8%
ARM05	Male	1 - 2	491	6554	74	12%	88%	Riparian	28%	11%	32%	28%
ARM06	Male	5 - 6	162	1959	19	84%	16%	Upland	11%	0%	21%	68%
ARM07	Male	4 - 6	597	7606	83	18%	82%	Riparian	39%	0%	17%	45%
ARM09	Male	8 - 9	461	6001	50	92%	8%	Upland	0%	0%	12%	88%
ARM10	Male	5	54	1211	8	53%	47%	Mixed	0%	0%	0%	100%
LM7	Male	4 - 5	151	920	15	96%	4%	Upland	0%	0%	0%	100%
SEVF01	Female	3 - 4	490	3866	19	100%	0%	Upland	0%	0%	5%	95%
SEVF02	Female	3	126	1072	12	3%	97%	Riparian	67%	0%	8%	25%
SEVF03	Female	3 - 4	563	3800	58	90%	10%	Upland	0%	0%	43%	57%
SEVF04	Female	5 - 6	512	5562	63	100%	0%	Upland	0%	0%	24%	76%
SEVM01	Male	5	27	341	3	51%	49%	Mixed	67%	0%	0%	33%

** The following male pumas were removed for bighorn depredation during this study: ARM01, ARM05, ARM06, ARM10, LM7. Male puma ARM04 was also removed due to public safety concerns because he was using human populated areas in Truth or Consequences, NM.*

Table 2: Prey kills documented at cluster sites from collared pumas at the Armendaris Ranch and Sevilleta National Wildlife Refuge in south-central New Mexico, from 2014 – 2018. Prey species were categorized into four classifications for the analysis; avian, aquatic, small mammal, and ungulate.

Prey Classification	Prey Species	No. Killed	Percent of Total Kill Sites	No. Prey Kills per Season			No. Prey Kills per Prey Sex			No. Prey Kills per Prey Age Class					
				Cool-Dry	Hot-Dry	Hot-Wet	Male	Female	Unidentified	Neonate	Yearling	Sub-adult	Adult	Mature	Unidentified
Avian	American crow (*Corvus brachyrhynchos*)	3	<0.5%	0	3	0	0	0	3	0	0	0	0	0	3
	Red-tailed hawk (*Buteo jamaicensis*)	1	<0.5%	1	0	0	0	0	1	0	0	0	1	0	0
	Rio Grande turkey (*Meleagris gallopavo intermedia*)	6	1%	0	2	4	2	0	4	0	0	1	3	0	2
	Various non-waterfowl species	8	1%	6	1	1	0	0	8	0	0	0	0	0	8
	Total Avian Prey Kills	**18**	**3%**	**7** **39%**	**6** **33%**	**5** **28%**	**2** **11%**	**0** **0%**	**16** **89%**	**0** **0%**	**0** **0%**	**1** **6%**	**4** **22%**	**0** **0%**	**13** **72%**
Aquatic	Beaver (*Castor canadensis*)	70	10%	34	14	22	2	0	68	0	0	2	44	2	22
	Common carp (*Cyprinus carpio*)	49	7%	9	22	18	0	0	49	0	0	0	5	0	44
	Channel catfish (*Ictalurus punctatus*)	1	<0.5%	0	0	1	0	0	1	0	0	0	1	0	0
	Muskrat (*Ondatra zibethicus*)	1	<0.5%	0	1	0	0	0	1	0	0	0	1	0	0
	Waterfowl	21	3%	11	3	7	0	0	21	0	0	0	5	0	16
	Spiny softshell turtle (*Apalone spinifera*)	16	2%	1	0	15	0	0	16	0	0	0	0	0	16
	Total Aquatic Prey Kills	**158**	**23%**	**55** **35%**	**40** **25%**	**63** **40%**	**2** **1%**	**0** **0%**	**156** **99%**	**0** **0%**	**0** **0%**	**2** **1%**	**56** **35%**	**2** **1%**	**98** **62%**
Small Mammal	Badger (*Taxidea taxus*)	7	1%	4	0	3	1	0	6	0	0	0	3	2	2
	Bobcat (*Lynx rufus*)	5	1%	1	3	1	0	0	5	0	0	0	2	0	3
	Desert cottontail (*Sylvilagus audubonii*)	3	<0.5%	2	0	1	0	0	3	0	0	0	0	0	3
	Coyote (*Canis latrans*)	84	12%	48	13	23	2	1	81	0	1	2	57	6	18
	Domestic dog	1	<0.5%	1	0	0	0	0	1	0	0	0	0	0	1
	Grey fox (*Urocyon cinereoargenteus*)	19	3%	2	0	17	0	0	19	0	0	1	5	0	13
	Jackrabbit (*Lepus californicus*)	5	1%	1	1	3	0	0	5	0	0	0	0	0	5
	Kit fox (*Vuples macrotis*)	1	<0.5%	1	0	0	0	0	1	0	0	0	1	0	0
	Porcupine (*Erethizon dorsatum*)	2	<0.5%	1	0	1	0	0	2	0	0	0	2	0	0
	Raccoon (*Procyon lotor*)	51	7%	35	3	13	3	1	47	0	1	8	21	0	21
	Ring tail (*Bassariscus astutus*)	1	<0.5%	1	0	0	0	0	1	0	0	0	0	0	1
	Skunk - Spotted (*Spilogale gracilis*), Striped (*Mephitits mephitis*), Hog-nosed (*Conepatus leuconotus*)	13	2%	8	4	1	1	0	12	0	0	0	2	0	11
	Total Small Mammal Prey Kills	**192**	**28%**	**105** **55%**	**24** **12%**	**63** **33%**	**7** **4%**	**2** **1%**	**183** **95%**	**0** **0%**	**2** **1%**	**11** **6%**	**93** **48%**	**8** **4%**	**78** **41%**
Ungulate	Bighorn sheep (*Ovis Canadensis nelsoni*)	27	4%	19	1	7	12	5	10	7	1	4	8	6	1
	Cattle (*Bos taurus*)	5	1%	4	1	0	0	0	5	4	0	1	0	0	0
	Elk (*Cervus canadensis*)	13	2%	3	2	8	3	6	4	0	2	5	6	0	0
	Feral goat (*Capra hircus Linnaeus*)	1	<0.5%	1	0	0	0	0	1	0	0	0	1	0	0
	Collared peccary (*Peccary tajacu*)	21	3%	14	2	5	0	0	21	0	0	3	17	0	1
	Mule deer (*Odocoileus hemionus*)	195	28%	74	11	110	38	40	117	37	36	24	68	11	19
	Gemsbok (*Oryx gazella*)	35	5%	18	10	7	3	0	32	7	5	13	3	0	7
	Pronghorn (*Antilocapra americana*)	21	3%	5	4	12	9	2	10	0	0	3	13	0	5
	Total Ungulate Prey Kills	**318**	**46%**	**138** **43%**	**31** **10%**	**149** **47%**	**65** **20%**	**53** **17%**	**200** **63%**	**55** **17%**	**44** **14%**	**53** **17%**	**116** **36%**	**17** **5%**	**33** **11%**
	Total Prey Kills	**686**	**100%**	**305** **44%**	**101** **15%**	**280** **41%**	**76** **11%**	**55** **8%**	**555** **81%**	**55** **8%**	**46** **7%**	**67** **10%**	**269** **39%**	**27** **4%**	**222** **32%**



Source: Esri, DigitalGlobe, GeoEye, Earthstar

Figure 1: Map of the two study areas in which kill site and diet data was collected from satellite-collared pumas; the Sevilleta National Wildlife Refuge (north), Armendaris Ranch (south) and Rio Grande riparian bosque habitat (blue) in southcentral New Mexico. Predation data was collected from collared pumas from 2016-2018 at the Sevilleta National Wildlife Refuge and from 2014-2018 at the Armendaris Ranch.

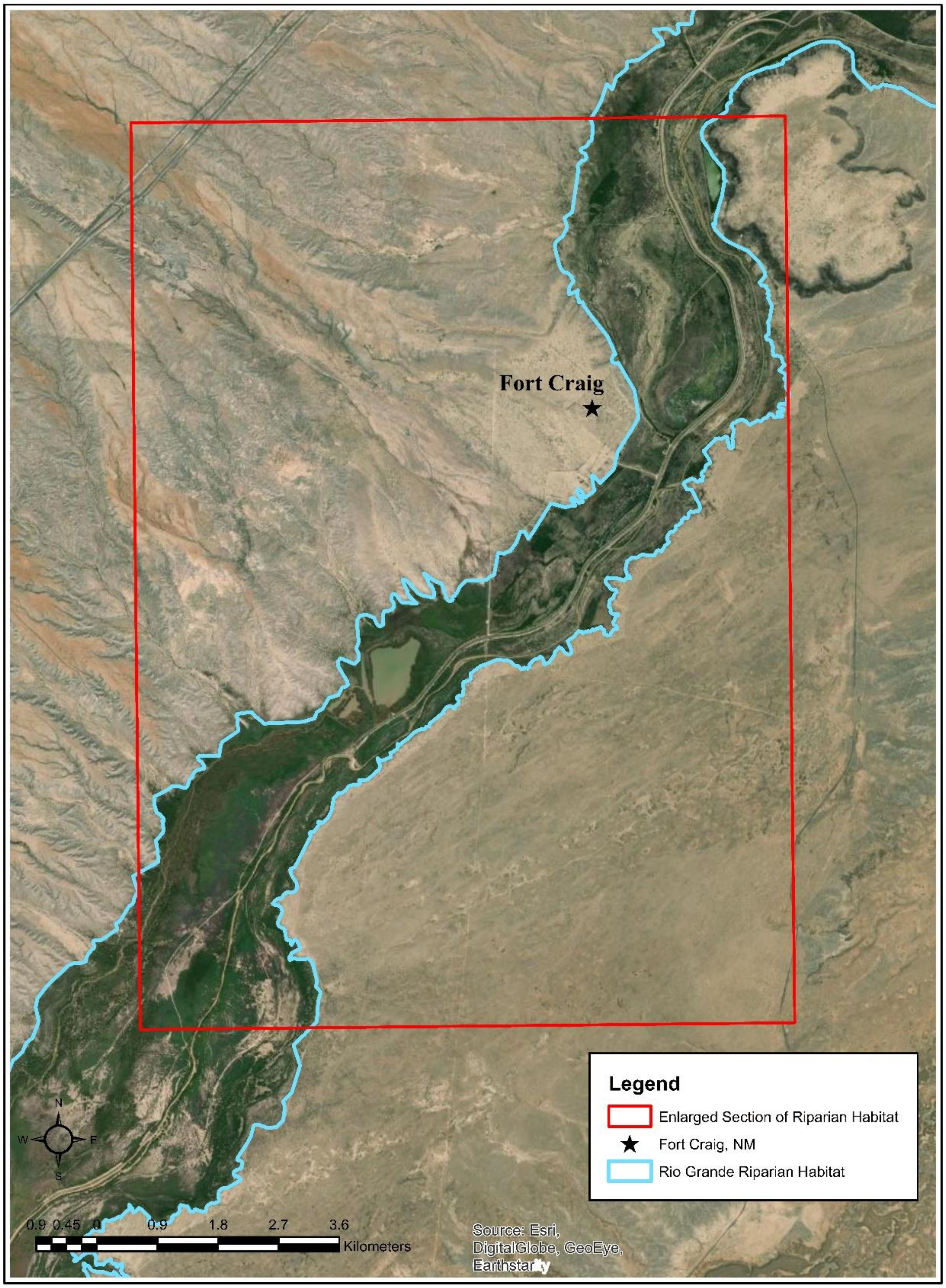


Figure 2: Enlarged section of Rio Grande riparian bosque habitat bordering the Armendaris Ranch near Fort Craig, NM in which kill site and diet data were collected from GPS-collared pumas from 2014 - 2018.

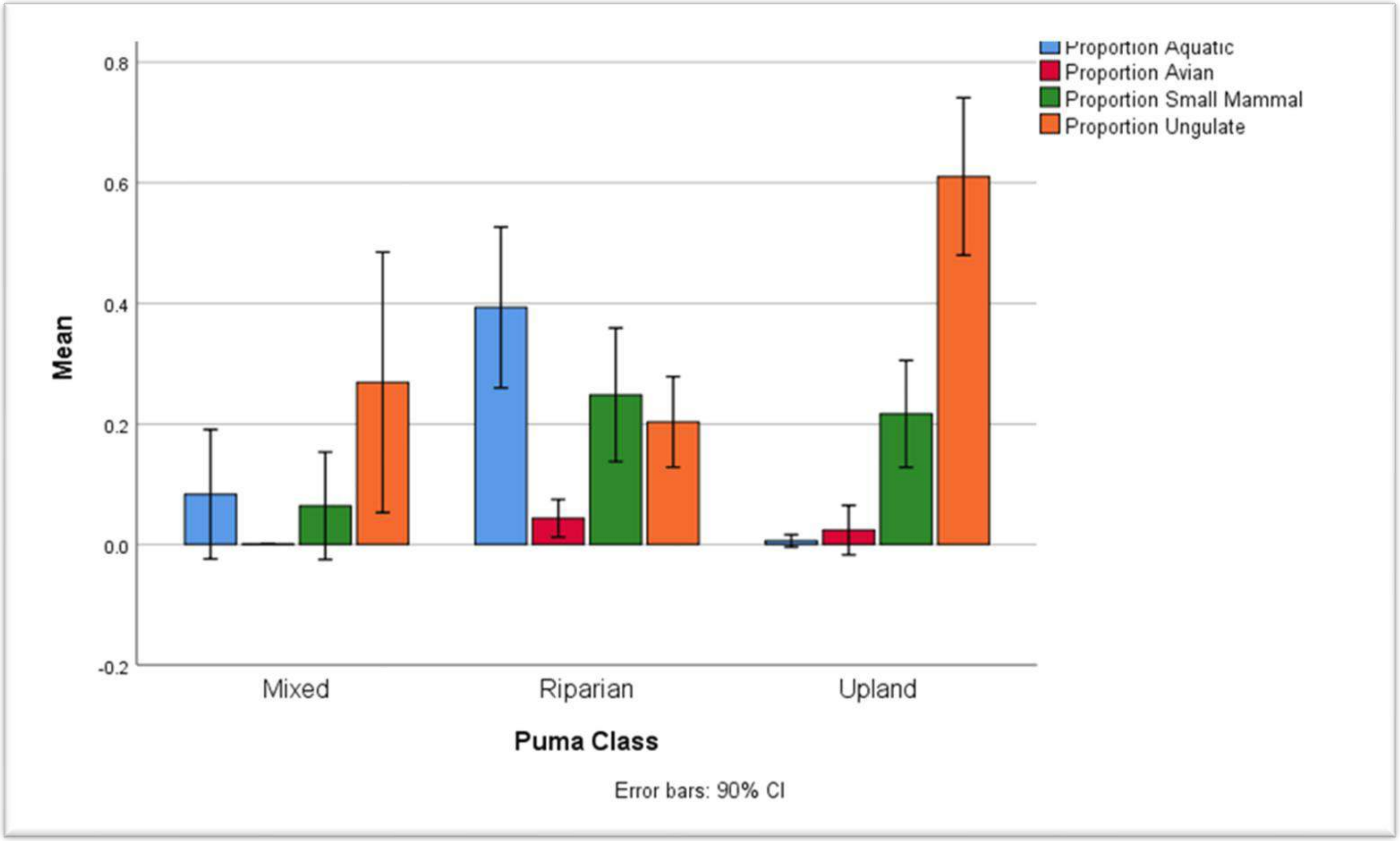


Figure 3: Proportions of prey classes in the diets of satellite-collared pumas in southern New Mexico from 2014-2018. Pumas are categorized into habitat classes based on the proportion of their GPS fixes within the upland desert and Rio Grande riparian bosque habitats at the Armendaris Ranch and Sevilleta National Wildlife Refuge.

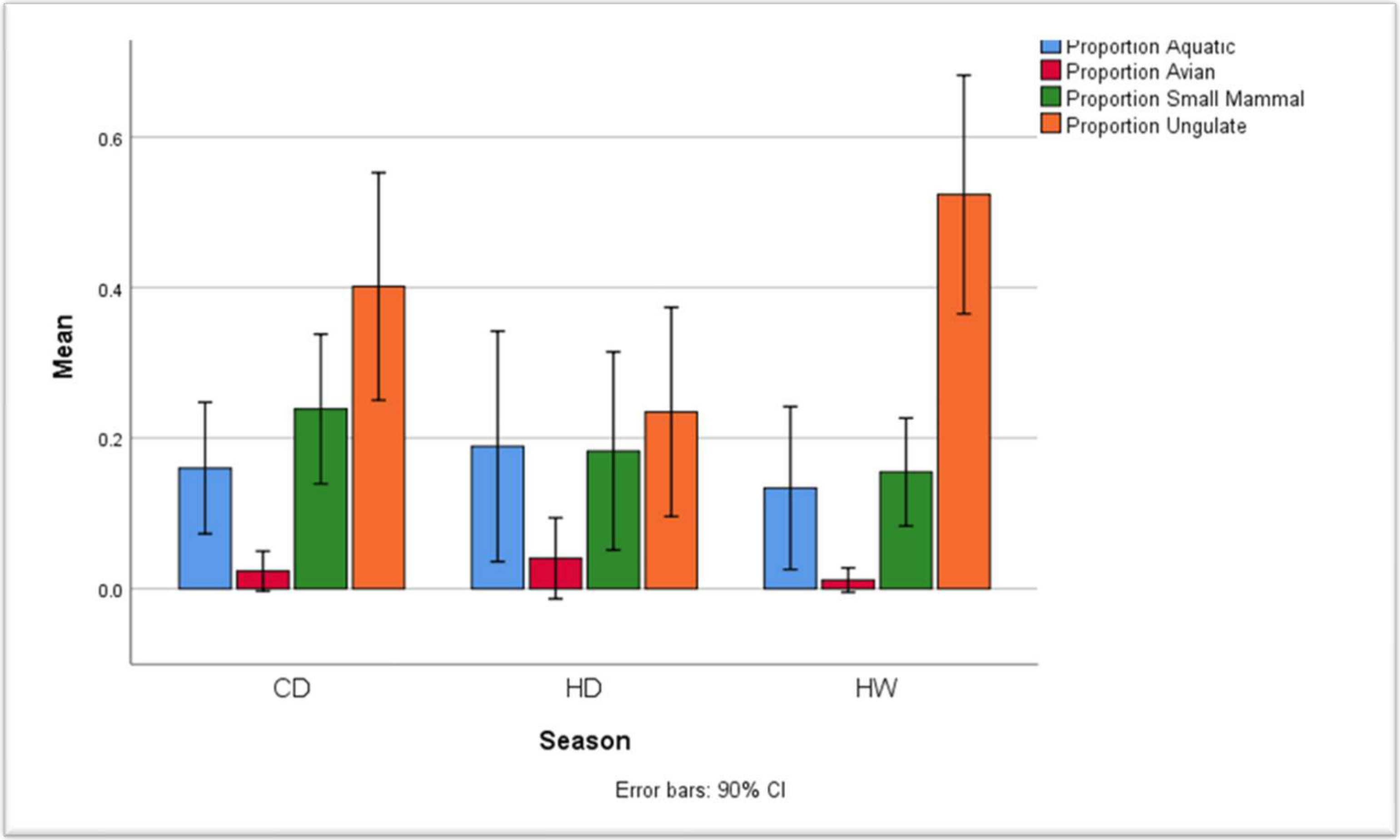


Figure 4: The proportions of prey classes per season in the diets of satellite-collared puma at the Armendaris Ranch and Sevilleta National Wildlife Refuge in southern New Mexico from 2014-2018. The seasons were determined based on long term climate data and classified as hot-dry (HD), cool-dry (CD), and hot-wet (HW).

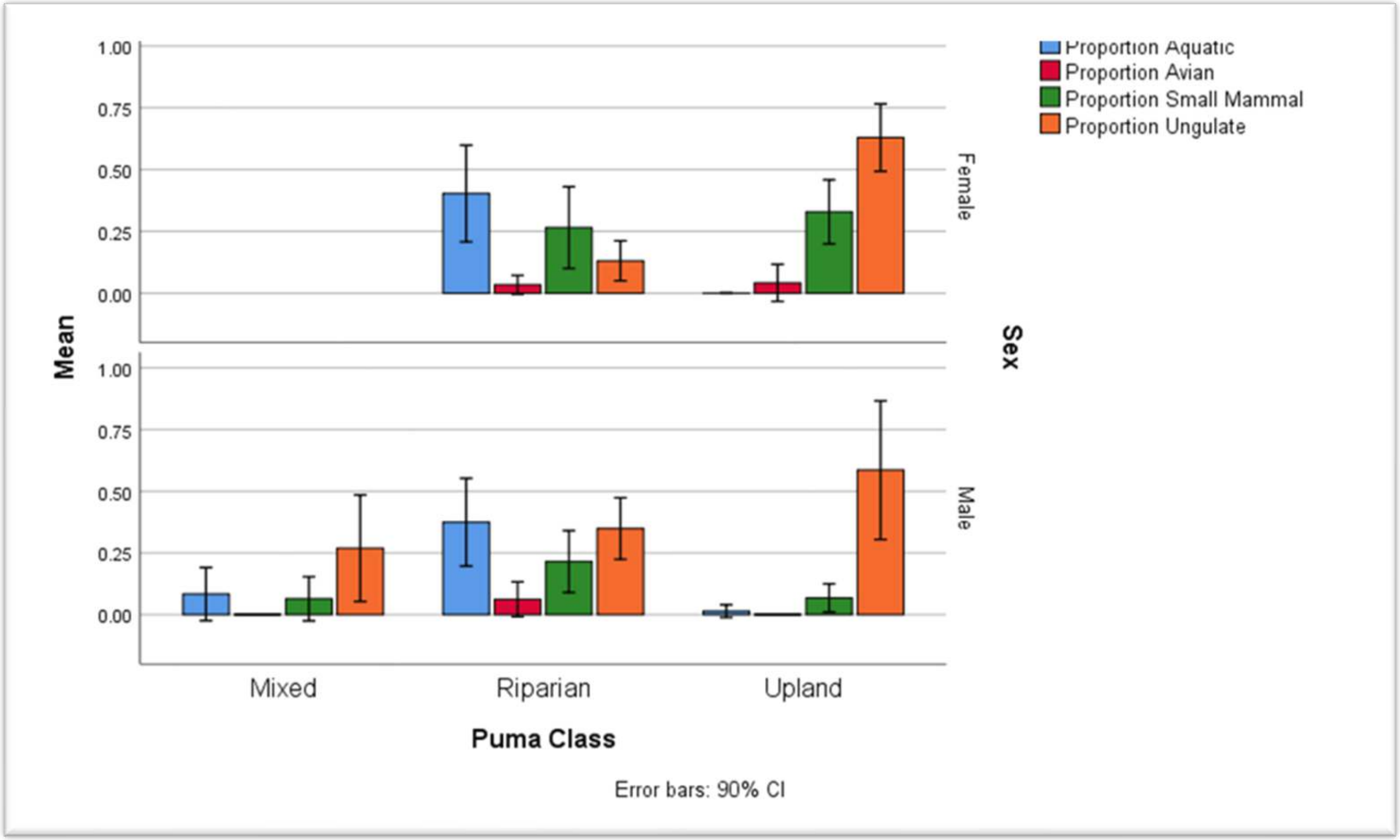


Figure 5: The proportions of prey classes in the diets of satellite-collared male and female puma at the Armendaris Ranch and Sevilleta National Wildlife Refuge in southern New Mexico from 2014 – 2018. The data is grouped by puma habitat classification based upon proportion of GPS fixes within the upland desert and Rio Grande riparian bosque habitats.

Chapter Two

The Influence of Man-made Water Sources on Puma Kill Site Locations

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ABSTRACT

Man-made water sources have been developed for wildlife in arid regions since the mid 1900's. Although wildlife are generally considered to benefit from water development, there is very little known about how the provision of man-made water influences predator-prey dynamics. It is possible that the increased abundance of prey and or the habitat features surrounding man-made water sources increase predation risk by puma (*Puma concolor*). To examine this, puma diet data was compiled from seven study areas in the Chihuahuan and Sonoran deserts to determine the influence of man-made water sources on puma habitat use and kill site locations. The proximities of ungulate kill sites to man-made water sources were compared with areas generally available within puma home ranges. Mixed effects logistic regression was used to determine if the probability of a site being a kill location was related to the proximity to water sources and or other habitat characteristics. While pumas did not appear to be exploiting the predictable prey visitation of man-made water sources, they were capitalizing on the restricted distribution of prey within 5 km of water sources. At the home range scale, puma use areas proximate to water sources that likely have increased prey abundance and higher probabilities of encountering prey for hunting. Within the home range, pumas select fine scale habitat features, such as woody cover, that enhance their ability to stalk, ambush, and effectively kill prey.

INTRODUCTION

Since the mid-1900s, State and Federal management agencies have built and maintained supplemental water sources (hereafter, man-made waters) for wildlife in arid regions where water is naturally deficient or where historically available perennial water sources have gone dry or have been reduced in availability (Russo 1956, Wright 1959, Blong and Pollard 1968, Broyles 1995). In the Chihuahuan and Sonoran desert regions of the southwestern United States, man-made water sources (i.e., guzzlers, catchments, retention dams) are often constructed to benefit game species such as desert bighorn sheep (*Ovis canadensis nelsoni*), deer (*Odocoileus hemionus, O. virginianus*), pronghorn (*Antilocapra americana*), and elk (*Cervus canadensis*; Smith and Krausman 1988, Wakeling et al. 2009, Cain et al. 2013); natural water sources (i.e., tinajas and springs) are also commonly modified to increase the duration of water availability and storage capacity. Rosenstock et al. (1999) reported that there were more than 6,000 man-made water sources distributed across the Southwest that are actively maintained by wildlife agencies. The cost of these water provisioning programs were estimated to exceed $1,000,000 annually in the late 1990s (Rosenstock et al. 1999). In addition to the water sources developed for wildlife, there have been countless water sources developed by the livestock industry across the southwestern United States. Although their purpose is for production and management of livestock, these water sources are also heavily used by wildlife, especially in arid regions (Rosenstock et al. 1999).

In spite of the extensive management of water sources for wildlife, there is ongoing debate over the construction and maintenance of man-made water and the impact that it has on wildlife and desert ecosystems (Broyles 1995, Krausman et al. 2006; Simpson et al. 2011). One concern is that developing man-made water sources to promote higher ungulate densities might inadvertently increase predation risk by subsidizing predators, such as puma (*Puma concolor*), allowing them to utilize areas that would otherwise have limited water and prey availability (Kittle et al. 2006; deBoer et al. 2010; Davidson et al. 2013). Therefore, artificially enhancing water availability in arid desert landscapes may encourage puma to spend more time in areas that they might not inhabit otherwise, potentially resulting in increased predation rates on ungulates and other prey species. Additionally, anecdotal observations of predation attempts by puma at man-made waters and observations of prey remains near drinkers have led some to speculate that pumas are using these water sources as ambush locations, thereby exacerbating predation risk for prey that utilize these waters (Rosenstock et al. 2004; DeStefano et al. 2000).

There are two primary mechanisms through which man-made water sources might influence predator-prey interactions in arid areas: the prey vulnerability hypothesis and the prey abundance hypothesis (Pennycuick 1975; Maddock 1979; Simpson et al. 2013). The prey vulnerability hypothesis implies that predators select for habitats that have increased stalking cover that enhances their ability to ambush prey. Whereas the prey abundance hypothesis suggests that predators select for habitats that have higher densities of preferred prey species (Simpson et al. 2013; Kittle et al. 2016). During dry seasons, availability of free water declines as ephemeral sources dry up, water demands increase, and many wildlife species can become spatially restricted, concentrating in areas proximate to the remaining perennial water sources (Thrash et al. 1995; Rosenstock et al. 2004; Harris et al. 2015). Numerous studies have shown that African lions (*Panthera leo*) utilize water sources for hunting due to the increased abundance and susceptibility of prey congregated at water sources during dry season (Loveridge et al. 2006; Davison et al. 2013). DeBoer et al. (2010) concluded that African lions selected for areas that contained higher prey densities, supporting the prey abundance hypothesis.

Conversely, others have concluded that African lions select hunting areas where they are more successful due to increased stalking cover, supporting the prey vulnerability hypothesis (Grant et al. 2005; Davies et al. 2016). Davidson et al. (2013) reported that African lions exhibit opportunistic hunting behavior with the locations of kills typically being within 2 km of a water source, indicating that the water sources might indirectly influence lion foraging behavior. Consequently, regardless of the mechanism (increased prey vulnerability or increased abundance) there is a strong association between kill sites of African lions and proximity to water sources in the dry season (Grant et al. 2005; de Boer et al. 2010).

Broyles (1995) suggested that man-made water sources in North American deserts might similarly exacerbate predation of native ungulates. Harris et al. (2015) reported that puma occurrence at and use of water sources on the Sevilleta National Wildlife Refuge near Socorro, New Mexico was strongly correlated with the presence of prey species at water sources, primarily pronghorn, deer, and elk. Whereas prey visitation to water sources was mostly related to aridity; low precipitation and relative humidity and high maximum daily temperatures (Harris et al. 2015). These findings suggest that puma predation in the arid regions of North America may be consistent with the prey abundance hypothesis, meaning that pumas utilize areas that concentrate prey, such as man-made water sources, for hunting because of the increased availability of prey during the dryer seasons. Contrary to the prey abundance hypothesis, O’Brien et al. (2006) documented 37,989 camera observation hours at water sources in the Sonoran Desert from 2000 to 2003 and only reported eight predation attempts made by raptors and bobcats (*Lynx rufus*). If man-made water facilitates puma predation on ungulates due to the distribution of prey near water sources or if pumas use man-made water sources to ambush drinking ungulates, the practice of providing man-made water to benefit game species could be a counterproductive management strategy. However, in spite of the research results on use of water holes by African lions to capture prey, there has been little research conducted in the Chihuahuan and Sonoran deserts to determine the efficacy of the provision of man-made water sources or the biological ramifications the practice might have on predator-prey dynamics (Ballard et al. 1998; Rosenstock et al. 2004; O'Brien et al. 2006; Simpson et al. 2011). Moreover, little is known about the water requirements of puma or how the availability of free water influences their behavioral ecology or spatial-temporal habitat use patterns in arid environments.

Clearly, more science is required to inform the management of man-made water sources, ungulates and puma in desert ecosystems. To examine the influence that man-made water sources might have on puma-prey interactions and kill site proximity to water sources, I compiled puma kill data from seven southwestern study areas varying in temperature, precipitation, aridity and availability of both natural and man-made perennial water sources. My objectives were to: 1) determine relationships between the locations of puma kills and proximity of man-made water sources; and 2) build upon this relationship by evaluating the influence that other environmental and topographical factors have on the timing and location of puma kill sites. Both of the predation hypotheses, prey abundance and prey vulnerability, have been supported by empirical evidence from previous studies on African lions (Grant et al. 2005; Kittle et al. 2006; deBoer et al. 2010). However, these two hypotheses are not necessarily mutually exclusive. Because of this, I expect puma kills in the arid Southwest to be influenced by the abundance of prey proximate to man-made water sources during dry seasons and by the amount of ambush cover available within the habitat.

STUDY AREAS

Chihuahuan Desert Areas

The Armendaris Ranch (AR) located 24 km east of Truth or Consequences New Mexico, is a 146,854 ha private bison ranch managed by Turner Enterprises. Elevations range from 1,340 m along the Rio Grande to 2,083 m in the Fra Cristobal Mountains. The landscape at the AR is comprised mostly of Chihuahuan Desert Scrub and xeric grasslands at lower elevations, with some sparse areas of pinyon-juniper (*Pinus edulis*, *Juniperus* spp.) woodlands at higher elevations in the Fra Cristobal Mountains. Additionally, there is a strip of riparian bosque habitat adjacent to the Rio Grande and edges of Elephant Butte Reservoir which borders the western boundary of the Armendaris. The mean annual precipitation at the Armendaris is 237 mm (SD ± 76) and mean annual snowfall is 86 mm (SD ± 155). Temperatures range from an average daily minimum of 5.3°C (SD ± 3.1) in January to an average daily maximum 30.6°C (SD ± 2.3) in July (climate data from Elephant Butte Dam, Truth or Consequences, NM; WRCC 2018a). Common prey species for pumas in the upland desert areas of the AR include mule deer (*Odocoileus hemionus*), coyote (*Canis latrans*), pronghorn (*Antilocapra americana*), gemsbok (*Oryx gazella*), and desert bighorn sheep (*Ovis canadensis nelsoni*) in the Fra Cristobal Mountains. Additional prey species within the riparian bosque habitat include beaver (*Castor canadensis*), common carp (*Cyprinus carpio*), raccoon (*Procyon lotor*), and various waterfowl species. The AR has few perennial springs, two in the flat grasslands and five within the Fra Cristobal Mountains. There are 168 man-made water sources developed for livestock ranching distributed throughout the Armendaris, primarily in the grassland areas. There are seven man-made water sources in the Fra Cristobal Mountains, including five water catchments and two modified springs that were constructed to benefit bighorn sheep in the Fra Cristobal Mountains.

I included modified springs with man-made water sources because they would only provide water seasonally for wildlife if they had not been enhanced by man-made structures.

The Ladder Ranch (LR) located approximately 12 km northeast of Hillsboro, New Mexico, is a 63,308 ha private bison ranch managed by Turner Enterprises. Elevation ranges from 1,402 m along the lower Animas Creek to 2,255 m in the Black Range Mountains bordering the Gila Wilderness. Vegetation types on the LR are comprised of Chihuahuan Desert Scrub and grasslands at lower elevations, pinyon-juniper woodlands at mid-elevations, and ponderosa (*Pinus ponderosa*) forest at higher montane elevations. Temperatures range from an average minimum of -3.9°C in January (SD ± 2.98) to an average maximum of 33.36°C in June (SD ±30.5). Mean annual precipitation is 315 mm (SD ± 98.6), of which 162 mm is snowfall (SD ± 228.3, climate data from Hillsboro, NM; WRCC 2016). Elk, mule deer, skunk (*Mephitis* spp.), and collared peccary (*Pecari tajacu*) are prey species that are commonly utilized by pumas on the LR. The LR has several perennial streams supplied by snow melt from the Black Range in the Gila Wilderness. There are also 318 man-made water sources such as wells, drinkers, and dirt tanks developed primarily for livestock but that are also to be utilized by wildlife including deer, elk, and endangered Chiricahua leopard frogs (*Lithobates chiricahuensis*).

The Sevilleta National Wildlife Refuge (SNWR) located 30 km north of Socorro, New Mexico, is a 93,077 ha wildlife refuge managed by U.S. Fish and Wildlife Service. Elevation ranges from 1,432 m along the Rio Grande to 2,529 m in the Pino and Ladrone mountains. Dominant vegetation types on the SNWR are comprised of Chihuahuan Desert Scrub, Great Plains Short Grass Prairie, and Colorado Plateau Shrub Steppe at lower elevations and then pinyon-juniper woodland at higher elevations. There is also a strip of riparian bosque habitat bordering the Rio Grande and La Joya wetland restoration areas bisecting the eastern and western parts of the SNWR. Temperatures range from an average daily minimum of 2.1°C (SD ± 4.3) in January to an average daily high of 25.2°C (SD ± 2.6) in July. Mean annual rainfall is 206 mm (SD ± 66), with mean annual snowfall of 118 mm (SD ± 122; climate data from Bernardo, NM: WRCC 2018). Mule deer, pronghorn, coyote, elk, and beaver are commonly utilized prey species. The SNWR has some perennial springs, including 4-Springs in the Ladrone Mountains, and a perennial stream, the Rio Salado, within its western half. Then there are a few perennial springs, including Cibola Spring, near the Pino Mountains within its eastern half. Historically, there were several man-made water sources developed for livestock ranching throughout the SNWR. However, after its transition to a National Wildlife Refuge in 1973, many of the livestock drinkers have been removed or converted to wildlife drinkers. Currently, there are approximately 54 man-made water sources within the SNWR study area.

Sonoran Desert Areas

The Kofa National Wildlife Refuge (KNWR) located approximately 100 km northeast of Yuma, Arizona, is a 269,277 ha wildlife refuge managed by the U.S. Fish and Wildlife Service. The elevation at the KNWR ranges from 275 m in the King Valley to 1,486 m atop Signal Peak in the Kofa Mountains. The KNWR is comprised primarily of Sonoran Desert Scrub including mesquite (*Prosopis juliflora*), scorpion weed (*Phacelia arizonica*), brittlebush (*Encelia farinosa*) and various cacti species such as prickly pear (*Opuntia* spp.), hedgehog (*Echinocereus* spp.), pincushion (*Escobaria* spp.), barrel (*Ferocactus* spp.), and the iconic saguaro (*Carnegiea gigantea*). Temperatures range from an average minimum of 8.28°C in January (SD ± 3.33) to an average maximum of 39.84°C in July (SD ± 1.99). The KNWR is extremely arid with the mean annual precipitation of 165 mm (SD ± 75.9) (climate data from Kofa Mine, AZ; WRCC 2016d). Mule deer, bighorn sheep, coyote, and burros (*Equus asinus*) are potential prey on the KNWR.

Many of the natural water sources (i.e., springs, tinajas) on the KNWR have been modified by man-made structures (i.e., retention dams, spring boxes, shade covers) to improve their ability hold water throughout the year. There are few remaining natural perennial water sources on the KNWR that have not been modified by a man-made structure. Including the modified natural water sources, there are approximately 131 man-made water sources developed for wildlife on the KNWR.

The Big Horn-Vulture Mountains study area (BHVM) located approximately 100 km west-northwest of Phoenix, Arizona is a large expanse of public and private lands utilized by pumas. The area contains multiple mountain ranges including the Big Horn, Vulture, Buckskin, Rawhide, Harcuvar, and Poachie Range mountains. The elevation ranges from in the 365 m in the Tonopah desert valley to 1731 m in the Harquahala Mountains. The landscape and vegetation are similar to the KNWR. Temperatures range from an average minimum of 2.67°C (SD ± 15.9) in January to and average maximum of 41.5°C (SD ± 16.54) in July. The landscape is extremely arid with the mean annual precipitation being 160.3 mm (SD ± 61.5) and no mean annual snowfall on record (climate data from Tonopah, AZ; WRCC 2020f). Mule deer, bighorn sheep, collared peccary, and feral burro are prey species utilized by pumas in the Big Horn-Vulture Mountains study area. There are very few perennial natural water sources that have not been modified or enhanced by man-made structures within the BHVM study area, but there are approximately 271 man-made water sources developed for livestock, mining, and wildlife management.

Non-desert Areas

The Gallinas Peak area located 16 km southwest of Corona, New Mexico, is part of the Cibola National Forest. The elevation ranges from 2,012 m in the basin to 2,600 m in the

Gallinas Mountains. The landscape at within the Gallinas Peak area is comprised of low elevation grasslands, pinyon-juniper woodland at mid-elevations, and ponderosa pine forests at higher elevations. The mean annual rainfall is 392.4 mm (SD ± 132) and mean annual snowfall is 926.3 mm (SD ± 481.8). Temperatures range from average minimum of -5.89°C in January (SD ± 4.87) and an average maximum of 28.7°C in July (SD ± 2.77; climate data from Corona, NM; WRCC 2016c). Mule deer, elk, barbary sheep (*Ammotragus lervia*), and porcupine (*Erethizon dorsatum*) are commonly preyed upon by pumas in the Gallinas Mountains. The Gallinas Mountains have a few perennial springs and approximately 43 man-made water sources developed for livestock ranching.

The Jemez Mountains are located approximately 14 km west of Los Alamos, New Mexico. The Jemez Mountains include the Valles Caldera National Preserve, which is a 36,104 ha National Preserve managed by the National Park Service. The Jemez Mountains are centered on the caldera of 1.25 million year old volcano and the elevation ranges from 2,440 m in the bottom of the caldera to 3,524 m atop Redondo Peak. There are montane meadows within the caldera and the surrounding landscape is comprised of pinyon-juniper woodlands and ponderosa and mixed conifer forests at higher elevations. Temperatures range from an average minimum of -7.6°C in January (SD ± 3.74) to an average maximum of 27.5°C in July (SD ± 2.47). Mean annual precipitation is 462 mm (SD ± 110.5), with an average annual snowfall of 1294.9 mm (SD ± 688.3), climate data from Los Alamos, NM; WRCC 2016e). The habitat in the Jemez Mountains supports densely populated prey species, such as elk and deer. Which supports denser populations of predators, such as pumas and black bear. There are several perennial streams, rivers, small lakes and springs within the Jemez Mountains. There are also approximately 291 man-made water sources utilized by both livestock and wildlife within the Jemez Mountains.

Based on long-term climate data, I classified seasons for all study areas as: the cool-dry (CD, November – March), hot-dry (HD, April – June), and hot-wet (HW, July – October) seasons.

METHODS

Capture and Data Collection

I captured pumas using foot-hold traps or trained hounds. Traps were set along game trails, scat sites, kill cache locations, or other areas that had an increased probability of puma occurrence. I used hounds to capture pumas in areas that provided suitable scent trailing conditions and safe escape structures (trees or boulders) for pumas. I immobilized captured pumas using 5 mg/kg ketamine combined with 0.08 mg/kg medetomidine and used 0.3 mg/kg atipamezole as the antagonist for medetomidine (Kreeger et al. 2002). I fitted captured pumas with a GPS-Iridium collar (Advanced Telemetry Systems G2110E or similar; Advanced Telemetry Systems, Isanti, MN). I programmed the collars to collect between one and sixteen GPS fixes per day and then to transmit the data from twice daily to every 72 hours. The variability in fix and transmission schedules is due to the older collar models (circa 2007) having reduced capabilities and battery life compared to the better performing newer models in later years as well as additional study objectives unique to each study area. All capture and handling procedures follow acceptable methods (Sikes et al. 2016) and were approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocol 2015-015).

I obtained puma diet composition data by investigating GPS clusters as potential kill sites in the field. The exact definition of a GPS cluster differed slightly between study areas. At the AR and SNWR, I defined clusters as being any location where a puma spent ≥ 6 consecutive crepuscular or nocturnal hours within a 50-m radius. The JM, LR, KNWR, BHVM, and GM projects defined clusters to be any location were a puma spent ≥6 hours within a 100-m radius. Essentially, any location in which a puma spent ≥6 consecutive hours within a 50-100 m radius was considered a cluster and subject to field visitation. I investigated clusters in the field as promptly as possible to prevent the loss of kill evidence caused by scavengers and weathering. I located kills at cluster sites by navigating to the centermost GPS fix within the cluster and then searching the surrounding area for evidence of a kill (i.e., carcass remains, hair, bone fragments, blood, drag marks, disturbed vegetation and soil; Shaw 1986). If a prey kill was located, I examined the carcass for evidence of puma predation such as bite marks to the neck or throat, carcass cache, subcutaneous hematomas on neck or throat, and puma tracks near carcass; I also used the rate of decomposition of the carcass relative to the GPS fix times and dates of the locations at the carcass site to determine if the animal was killed by a puma or died by some other cause and was then scavenged by a puma. I collected data on prey species, sex, age class, and carcass location at each kill site located. I identified prey sex by genitalia or secondary sexual characteristics when possible and estimated prey age class by tooth wear, pelage patterns, and the morphometric characteristics of the carcass (Heffelfinger 2010).

I obtained the locations of perennial water sources, both natural and man-made, from maps, historical records, satellite imagery, field observations, and GIS data. Most of the study areas kept updated records, maps, or GIS data of water developments within their boundaries. However, pumas often utilized public and private lands surrounding the study areas that had few records and had developed water sources for livestock production. For these areas, I gathered records from local BLM and NRCS offices as well as historical county records. For areas that lacked sufficient data, I marked water sources with a handheld GPS unit while investigating clusters in that area or using satellite imagery in ArcGIS (ESRI 2018: Release 10.6. Redlands, CA) for areas in which I did not have access. I included natural water sources (i.e., springs, tinajas) that had been modified or enhanced by man-made structures (i.e., retention dams, roof to prevent evaporation) with man-made water sources for all analyses. I then used ArcGIS to create shapefiles containing all of the known perennial water sources for each study area.

The riparian bosque habitat bounding both sides of the Rio Grande at the Armendaris and Sevilleta study areas resulted in diverse habitat conditions and increased diversity of potential prey species for pumas. At these two study areas, some pumas preferred to utilize the riparian bosque habitat, others predominantly used xeric upland desert areas, and some pumas utilized both areas, regularly moving between riparian bosque and upland desert areas. To account for variation in composition of available prey species related to the predominant use of one vegetation cover type over others, I used satellite imagery in ArcGIS to digitize the boundary between the riparian bosque vegetation along the Rio Grande and the more xeric upland deserts. I then classified pumas as being riparian, upland, or mixed based upon the proportion of their total GPS fixes within the upland and riparian areas: pumas with more than 75% of their cumulative fixes within the riparian area were classified as riparian, pumas with more than 75% of their cumulative fixes in the upland areas were classified as upland, and pumas with less than 75% of their cumulative fixes in either riparian or upland areas were classified as mixed. The majority of kills made by riparian pumas were near natural water sources, especially kills containing aquatic prey species (i.e., beaver, carp, waterfowl). To prevent bias in our analyses, I omitted data from pumas classified as riparian from the analyses.

To determine if the spatial distribution of puma kill sites were associated with the locations of perennial water sources, or other environmental factors, I created random points for comparison. I used Home Range Tools (HRT) Version 2.0.20 (Rodgers et al. 2015) in ArcGIS

10.6 to calculate a 90% kernel home range based upon the GPS collar data from each puma. I then randomly distributed points within each puma home range using a ratio of 20 random points for each kill location. I then replicated the data derived from the documented puma prey kills (i.e., prey species, age class, sex, date, season, puma ID, puma sex, puma age) 20 times and randomly assigned it to the randomly generated points for each puma to create a balanced data set.

Using the map of known man-made (and modified natural) perennial water sources, I calculated the Euclidian distance between each random point and kill location and the nearest man-made water source. Pumas often drag their prey from the point of ambush, or kill to the nearest concealment cover (i.e., brush, cave, trees, tall grass, boulders) before feeding on the carcass (Logan and Sweanor 2001). In many instances, the actual kill location or where the animal was attacked and killed is difficult to find in the field. Because of this, the carcass location or the site in which the carcass was fed upon and cached is often recorded as the kill site location in the data. The distance between the actual kill location and the carcass cache varies but is often within 100 m for larger prey items such as ungulates (Beier et al. 1995). To account for variability in habitat characteristics between the kill and carcass locations, I used ArcGIS to create 100 m buffers around all of the kill and random point locations. I then used the buffer areas to extract habitat characteristics at kill sites and random points using ArcGIS. I used Focal Statistics tools in ArcGIS to calculate the arithmetic mean of the cell values within the 100 m buffers for the continuous variables and the majority cell value within the buffers for the categorical variables for the analysis.

I included elevation, slope, northness, terrain ruggedness, vegetative characteristics, visibility, woody cover and drought indices in the analyses to evaluate if they influenced the spatial distribution and prey composition of puma kills. I used the LANDFIRE Data Access Tool Version 2.7 to obtain 30 x 30 resolution digital elevation models (DEM) for each study area. I then used ArcGIS to create percent slope and northness (i.e., cos(aspect)) raster layers from the DEMs; northness values ranged from 1 to -1 with values closer to 1 indicating north facing slopes. I used the Benthic Terrain Modeler 3.0 tool extension (Walbridge et al. 2018) calculate vector terrain ruggedness (VRM) using the DEM layers. I then extracted the mean value for elevation, percent slope, northness, and VRM within each 100 m buffer around the random locations and kill sites. I used LANDFIRE data to create raster layers containing vegetative cover, vegetative type, and vegetative height for each of the study areas. I then extracted the majority values within the 100 m buffers for each vegetative variable and then combined the multiple values into broader classifications that were more meaningful for my analyses; categories were determined based on vegetation structure rather than species composition because structure of vegetation is more related to stalking cover for pumas than species composition and it allowed for comparisons across study areas with disparate vegetation types and species composition. I classified vegetative cover values as barren, herbaceous cover (including agriculture), shrub cover <25%, shrub cover >25%, tree cover <20%, tree cover >20%, and other (developed, water, mining). I classified the values for estimated vegetative type as herb (including herbaceous cover, grasslands, agriculture fields), shrub (including shrubland, chaparral, desert scrub), and forest (including forest, woodland). I classified the values for estimated vegetative height as barren and herbaceous, shrub height <0.5m, shrub height >0.5m, and other (developed, water, mining). To determine visibility associated with topographic relief at each study area, I used model builder and the Visibility function in 3D Analyst Tools in ArcGIS along with the DEM to iteratively calculate the percentage of visible area within 100 m of each kill or random point. To estimate woody cover, I used 4 band imagery from the National Agriculture Imagery Program (NAIP) and the Imagery Classification tools in ArcGIS. Briefly, I first calculated NDVI from NAIP images, I then decomposed NAIP images into their separate color bands, and created a texture raster from the green and near infrared color bands using focal statistics with a 3 x 3 moving window. I then use these 7 inputs (NDVI, four individual color bands, and 2 texture layers) to classify woody cover using unsupervised classification within ArcGIS Image Classification (Zang 2001, Hoppus et al. 2002, Behee 2012). Then I used model builder in ArcGIS to extract the percentage of woody cover within the 100 m buffer at each kill or random location. I obtained historical drought indices (e.g., palmer drought severity index, average temperature) for each study area from the National Climate Data Center (2007 - 2018) and matched the drought and temperature conditions at each site based on the date each kill occurred. The drought indices that I initially included were Palmer drought severity index (PDSI), average temperature (TAVG), z index (ZNDX), Palmer monthly drought index (PMDI), minimum temperature (TMIN), and maximum temperature (TMAX).

This study focused on larger prey animals. The ungulate species included in the analysis were bighorn sheep, mule deer, gemsbok, elk, javelina, feral burro, feral horse, pronghorn, and barbary sheep. I excluded data describing avian, aquatic, and small mammal prey kills. I also excluded data from pumas that were represented by <5 five kill sites.

Data Analysis

Prior to analysis, I assessed data for multicollinearity using Spearman’s rank correlation coefficients. When two variables were highly correlated ($\rho \geq 0.60$), I removed one from the analyses keeping the variable that seemed more relevant to puma predation and was not correlated with other variables. All remaining continuous covariates were then standardized by subtracting the mean and dividing by the standard deviation, thus allowing for a more direct comparison of coefficients among variables that originally were on different scales of measurement. The continuous covariates that I included in the statistical analyses were Palmer Drought Severity Index (PDSI), average temperature (TAVG), woody cover, visibility, distance to man-made water, and VRM; categorical covariates included in the analysis were season, study area, estimated vegetation type (EVT), and prey species. I excluded many of the drought indices because they were highly correlated. Palmer drought severity index and average temperature were included because I expected the proximity of kills to water to be closest during hotter and dryer periods. Elevation, slope, and northness were highly correlated with the drought indices, woody cover, and vegetation covariates and were therefore omitted. I excluded other LANDFIRE vegetation covariates (i.e., estimated vegetative cover, estimated vegetative height) because they were not independent of vegetation type.

To determine if proximity to man-made water sources was associated with kill site locations, I developed a set of a priori model structures that included distance to man-made water sources and other habitat characteristics that could contribute to predation risk for prey species and or contribute to stalking cover for pumas (Table 2). I subset the data into 7 different data sets: combined study areas, Sonoran Desert areas only (KNWR, BHVM), Chihuahuan Desert areas only (AR, SNWR, LR), combined desert areas (AR, KNWR, BHVM, SNWR, LR), non-desert (JM, GM), only deer kills at all study areas, and only bighorn kills at study areas with bighorn sheep (KNWR, BHVM, AR, SNWR).

I then used mixed-effects logistic regression to determine if the probability of a site being a kill location was related to the proximity to man-made water and or other habitat characteristics using the blme package (Dorie 2014) in program R (R Core Team 2020) with puma ID entered as a random intercept. For the categorical covariates, I used Jemez as the reference level for study area, forest as the reference level for estimated vegetative type, hot-dry as the reference level for season, and mule deer as the reference level for prey species. Because determining if man-made water sources influence puma kill site locations was one of my primary objectives, I included distance to man-made water sources in most of the models. I included season, PDSI, and average temperature as interaction terms in some of the models because water requirements of prey fluctuates across seasons and climatic periods, but should be highest during the hotter and drier seasons and during periods of extended drought (Harris et al. 2015), therefore the relationship between kill sites and proximity to water sources could vary depending on drought and temperature conditions. If pumas are exploiting the increased prey density near water sources or otherwise using man-made water sources as ambush sites, the probability of a site being a kill proximate to water should increase during hotter and drier periods. Woody cover, terrain ruggedness, estimated vegetative type, and visibility were included as interaction terms in some of the models to assess if increased stalking or ambush cover influenced the probability of a kill both independently and as an interaction with distance to man-made water. Woody cover ranked highly in most of the preliminary model results, so I also developed some models that included woody cover without distance to man-made water to determine if woody cover had a greater influence on the probability of a kill than water sources.

I used Akaike's Information Criterion corrected for small sample size (AIC_c) to rank models and assess model support (Burnham and Anderson 2002). I considered any models with a $\Delta AIC_c \leq 2$ to be competing models, but considered any models with ΔAIC_c from 2 to 7 to have some support. I then evaluated the performance of each of the highest-ranking seasonal models using *K*-fold cross-validation (number of partitions, $K = 4$; bins = 30; repetitions, nrepeat = 50;

Boyce et al. 2002) in Program R (R Development Core Team 2020). Finally, I calculated variance inflation factors (VIFs) to determine if any of the most supported models were influenced by multicollinearity; VIF scores > 5.0 were considered to be indicative of models with potential multicollinearity issues.

RESULTS

Prey Composition and Kill Proximity to Man-Made Waters

Diet and spatial data were collected from 82 collared pumas from 2007 through 2018. There were 1,556 documented ungulate kills and 31,120 random locations distributed within puma home ranges. There were 483 kills in the Big Horn – Vulture Mountains, 144 kills at the Armendaris, 121 kills at the Gallinas Mountains, 225 kills at the Jemez Mountains, 259 kills at the Kofa, 225 kills at the Ladder, and 99 kills at the Sevilleta (Table 1). The majority of the kills were mule deer (*n* = 901, 58%), followed by elk (*n* = 287, 18%), bighorn (*n* = 145, 9%), collared peccary (*n* = 135, 9%), gemsbok (*n* = 35, 2%), pronghorn (*n* = 26, 2%), feral burro (*n* = 18, 1%), feral horse (*n* = 6, <0.01%), and barbary sheep (*n* = 3, <0.01%). The age class of the prey kills were predominantly adult (*n* = 609, 39%) but closely followed by neonates (*n* = 392, 21%), subadults (*n* = 186, 12%) with 369 unidentified (24%). Most of the kills occurred during the cool-dry season (*n* = 714, 46%), then the hot-wet season (*n* = 494, 32%) and lastly the hot-dry season (*n* = 348, 22%; Table 1).

Kills occurred closer to man-made water sources during the hot-dry seasons at most of the study areas, the exceptions being the Jemez Mountains and the Ladder Ranch which have an increase in ephemeral water during the hot-dry season due to snow melt runoff. Collared peccary kills occurred the closest to man-made water sources (mean 1,896 m, SD ± 1,269 m), followed by pronghorn (mean 2,213 m, SD ± 1,385 m), elk (mean 2,442 m, SD ± 2,393 m), bighorn (mean 2,467 m, SD ± 1,615 m), mule deer (mean 2,906 m, SD ± 2,733 m), and gemsbok (mean 3,122 m, SD ± 1,400 m). Barbary sheep kills occurred the furthest from manmade water sources (mean 16,154 m, SD ± 3057 m), followed by feral horse (mean 7,110 m, SD ± 3,720 m) and feral burro (mean 5,911 m, SD ± 3,376 m; Figure 2). Kills were closer to man-made water sources than the randomized points at all of the desert study areas; the randomized points were closer to water at the two non-desert study areas; Jemez and Gallinas (Figure 3). The mean distance from kills to man-made water sources was >2 km at all study areas except the LR where the mean distance from kills to man-made water sources was 1,148 m (SD ± 819 m; Figure 3). The mean distance from kills to man-made water for the other study areas were 2,214 m (SD ± 1,176 m) at the SNWR, 2,721 m (SD ± 2,291 m) at the BHVM, 2,747 m (SD ± 1,148 m) at the KNWR, 2,933 m (SD ± 2,529 m) at the JM, and 2,936 m (SD ± 1,764 m) at the AR. The mean distance from kills to man-made water at the Gallinas were 3,498 m (SD ± 4,748 m) as the GM study area had the fewest man-made water sources (*n* = 43). The mean distance from the random points to water sources were 2,885 m (SD ± 2,026 m) at the SNWR, 3,651 m (SD ± 3,357 m) at the BHVM, 4,737 m (SD ± 3,088 m) at the KNWR, 2,431 m (SD ± 2,040 m) at the JM, 3,249 m (SD ± 4,114 m) at the GM, 2,349 m (SD ± 2,389 m) at the LR, and 3,362 m (SD ± 1,961 m) at the AR. The mean distributions of man-made water sources within the cumulative puma 90% kernel home at each study area were: 1,539 m at the JM (SD ± 1,139 m), 3,445 m (SD ± 2,194 m) at the AR, 3,659 m (SD ± 3,372 m) at the LR, 5,635 m (SD ± 5,983 m) at the BHVM, and 5,988 m (SD ± 3,884 m) at the KNWR, 9,147 m (SD ± 7,766 m) at the SNWR, and 9,900 m (SD ± 9,117 m) at the GM.

Of the 1,556 ungulate kills documented, 1.2% (*n* = 20) of the total kills occurred within 100 m, 1.8% (*n* = 29) occurred between 100 - 250 m (3% of total kills were within 250 m), 5% (*n* = 78) occurred between 250 - 500 m (8% of total kills were within 500 m), 231 kills between 500 - 1000 m (15%; 23% of total), 450 kills between 1-2 km (29%; 52% of total), 260 kills between 2-3 km (17%; 69% of total), and 263 kills between 3-5 km (17%; 86% of total < 5 km) of a man-made water source (Figures 4 and 5). There were 225 kills that occurred further that 5 km from man-made water sources (14%; Figure 4). Mule deer comprised 75% (*n* = 15) of the kills within 100 m of a man-made water source and 54 % (*n* = 68) of the kills within 500 m of a water source, followed by elk 28% (*n* = 36), bighorn 11% (*n* = 14) and collared peccary 7% (*n* = 9). Conversely, mule deer comprised 63% (*n* = 142) of the kills located > 5 km from man-made water sources. The other prey species with kills > 5 km from man-made water included elk 17% (*n* = 42), bighorn 6% (*n* = 13), feral burro 4% (*n* = 8), with barbary sheep, collared peccary, gemsbok, feral horse and pronghorn having fewer than 5 kills each comprising 8% (*n* = 19).

Logistic Regression Models

All study area subset.–The highest ranking model using data from all study areas had overwhelming support compared to the other a priori models (w_i = 0.995; Table 4). The most supported model indicated that the probability of a location being a kill site was related to distance to man-made water, woody cover, and drought severity (PDSI; Table 4). Notably, the models with prey species and study area interactions were not among the most supported models. The main effects of the highest ranking model indicated that the probability of a site being a kill site generally decreased with increasing distance to man-made water sources and increased with increasing woody cover; confidence intervals for the coefficient for PDSI included 0 (Tables 4 and 5). However, there was also a significant 3-way interaction between distance to water, drought severity and woody cover. At the lowest levels of woody cover, the probability that a site was a kill site decreased with increasing distance to man-made water sources for all levels of PDSI (Figure 6), as woody cover increased, the probability that a site was a kill site increased with increasing distance to man-made water sources during periods with PDSI scores near and above the long-term mean (i.e., periods of normal and high precipitation); during periods with PDSI scores below the long-term average (i.e., dry periods), the probability that a site was a kill site decreased with increasing distance to man-made water sources regardless of changes in woody cover (Figure 6). The predictive performance from *K*-fold cross-validation for this model was very high ($\rho = 0.95$) and the VIF scores ranged from 1.15 to 1.55 for all of the model variables.

Sonoran Desert study areas.–There were three competitive models for ungulate kills at the Sonoran desert study areas (Table 3). Variables in the competitive models included distance to water, PDSI, wood cover and TAVG. The top-ranking model ($w_i = 0.422$) had 42-75% more support than the second ($w_i = 0.297$) and third ($w_i = 0.241$) highest ranking models (Table 3) and included distance to man-made water, woody cover and an interaction term between distance to man-made water and woody cover. The second highest ranking model included distance to man-made water sources and woody cover without an interaction term and the third ranking model included distance to man-made water sources, woody cover and TAVG, as well as a 3-way interaction between these covariates. Model-averaged parameter estimates from the covariates in these three models indicate that in the Sonoran Desert study areas, the probability of a site being a kill decreased with increasing distance to man-made water and increased with increasing woody cover, especially during hotter periods (Figure 7). The *K*-fold predictive performance estimation for these three models was good (ρ ranged from 0.88 to 0.91) and all VIF scores were ≤ 2.01.

Chihuahuan Desert study areas.–The top ranking model for ungulate kills at the Chihuahuan Desert study areas had overwhelming support ($w_i = 0.997$) and included distance to man-made water, visibility, and an interaction term between distance to man-made water and visibility. In the Chihuahuan Desert, the probability of a site being a kill decreased with increasing distance to man-made water sources and decreased with increasing visibility; and the effect of distance to man-made water generally increased with decreasing visibility (Figure 8) but the confidence intervals for the parameter estimate for the interaction term included 0. The predictive performance for this model was good (ρ = 0.85) and all VIF scores were ≤ 2.11.

Non-Desert study areas.–There were two competitive models for the non-desert study areas (Jemez and Gallinas mountains), although the highest ranking model had twice as much support (i.e., $w_i = 0.589$ vs. $w_i = 0.273$). Both models included distance to man-made water and woody cover, while the second ranking model also included PDSI. In the non-desert study areas, the probability of a site being a kill decreased with increasing distance to man-made water and increased with increasing woody cover and the influence of distance to water became more pronounced with increasing woody cover (Figure 9; Table 4). Proximity to manmade water sources increased in areas that had more woody cover, especially during dryer periods (Figure 10). However, both of the top ranking models from the non-desert areas had much lower predictive performance (i.e., K-fold ρ ranged from 0.24 to 0.36) and VIF scores were ≤ 2.04.

Desert study areas.–There were two competitive models for ungulate kills in the desert study areas, although the highest ranking model had over 3 times the support ($w_i = 0.647$) as the second highest ranking model ($w_i = 0.212$; Table 3). The top ranking model included distance to man-made water, woody cover and an interaction term between distance to man-made water and woody cover (Table 3); the second ranking model included distance to man-made water, TAVG, woody cover and a 3-way interaction term. In the combined desert areas, the probability of a site being a kill decreased with increasing distance to man-made water and increased in areas with more woody cover during higher average temperatures (Figure 11). Both of the top models had good predictive performance (i.e., *K*-fold ρ ranged from 0.81 to 0.82) and VIF scores were ≤ 1.52.

Mule deer kills only.–The highest ranking model for only mule deer kills at all of the study areas held overwhelming support compared to the other a priori models (w_i = 0.998; Table 3). Analogous to the highest ranking model for the all study area subset, the most supported model for mule deer kills indicated that the probability of a location being a kill site was related to distance to man-made water, woody cover, and drought severity (PDSI; Table 4 and 5). The interaction between distance to water, drought severity and woody cover indicated that at the lowest levels of woody cover, the probability that a site was a kill site decreased with increasing distance to man-made water sources for all levels of PDSI (Figure 12), as woody cover increased, the probability that a site was a kill site increased with increasing distance to man-made water sources during periods of normal and high precipitation; during dry periods, the probability that a site was a kill site decreased with increasing distance to man-made water sources regardless of changes in woody cover (Figure 12). The predictive performance for this model was very high (ρ = 0.98) and the VIF scores ranged from 1.08 to 1.45 for all of the model variables.

Desert bighorn sheep kills only.–There was high model selection uncertainty and four competitive models for bighorn sheep kills at desert study areas that had bighorn sheep populations (KNWR, BHVM, AR, and SNWR). The top ranking model ($w_i = 0.142$) and included distance to water without an interaction terms. The second ranking model ($w_i = 0.121$) included an interaction term between distance to water and season. The third ranking model ($w_i = 0.117$) and had an interaction term between distance to man-made water, TAVG, and woody cover. The fourth ranking model's weight was 0.094 and had an interaction term of distance to water x woody cover. For bighorn sheep, the probability of a site being a kill increased at closer proximities to water in areas with more woody cover and varied across seasons. The probability of a site being a kill near water sources was highest during the hot-dry season. For all seasons, the probability of a site being a kill decreased with increased distance from man-made water sources (Figure 13). All of the top four models had good predictive performance (i.e., *K*-fold ρ ranged from 0.79 to 0.90), and the VIF scores ranged from 1.12 to 3.87.

DISCUSSION

My results indicate that the locations of puma kills are influenced by proximity to man-made water sources and habitat characteristics, primarily ambush cover and that these relationships are influenced by climatic conditions, providing supportive evidence for both the prey vulnerability and prey abundance hypotheses. The mean distance between puma kill sites and man-made water were 13 – 51 % closer than the random locations of available habitat within puma home ranges within the desert study areas. However, the mean distance of both random locations and kill sites were $\geq 3{,}332$ m across all study areas and $\geq 3{,}502$ m in the desert study areas. Only 3% of kills were within 250 m and 8% of total kills within 500 m of a man-made water source, suggesting that there is not a significant amount of puma predation on ungulates at man-made water sources. Therefore, pumas do not appear to be using man-made water sources as sites to ambush prey.

I did find relatively consistent relationships suggesting that the probability of a site being a kill site (vs. a random site within the home range) declines with increasing distance to man-made water sources. The top models for the all of the datasets included distance to water as a predictor variable. These results suggest that the primary mechanism driving the influence of water sources on the location of lion kills is likely through the influence of water sources on the distribution of prey species on the landscape rather than lions using water sources as a means to locate and kill prey. In arid environments, studies have consistently shown that the distribution of prey species is strongly associated with water sources (Rosenstock et al. 1999) including desert bighorn sheep (McCarty and Bailey 1994; Wakeling and Miller 1989; Turner et al. 2004) and desert mule deer (Rautenstrauch and Krausman 1989; Hervert and Krausman 1986; O'Brein et al. 2006). Both desert bighorn sheep and mule deer are generally found within 4 km of water sources, and this decreases to 0.5 – 3.1 km during the summer (McCarty and Bailey 1994; Krausman et al. 1995; Turner et al. 2004). The influence of water sources on the distribution of prey species likely explains the results I found when assessing the proximity of kill sites to man-made water sources. For example, Cain et al. (2008b) reported that the mean proximity of GPS-collared bighorn sheep to water catchments ranged from 2,456 m to 2,910 m in southwestern Arizona, which is consistent with our findings of the mean proximity of bighorn kills to man-made water being 2,467 m. Krausman et al. (1995) reported that the mean distance of desert mule deer locations to water catchments ranged from 1.9 km to 3.3 km in the Big Horn-Vulture mountains area, which is also consistent with our findings of the mean proximity of mule deer kills being 2.8 km from man-made water sources within the BHVM area and 2.9 km at all of the combined study areas. Davidson et al. (2013) reported that African lions typically kill prey 1 – 4 km from a waterhole, preferentially within 2 km of a waterhole. The pumas in this study exhibited similar behavior as 29% of the kills occurred between 1 – 2 km of a water source and 86% occurred within 5 km of a water source. In general, puma kills were closest to man-made water sources during periods when we would expect prey to be spatially restricted to and more abundant near water sources during the dry seasons (Rosenstock et al. 1999).

Stalking cover is a critical component for pumas to be able to successfully capture prey (Hornocker 1970). Therefore, pumas select for areas that have suitable stalking cover (Laing 1988; Sunquist and Sunquist 1989; Hornocker 1970). Some studies have reported puma using topographic features and rugged terrain to stalk their prey (Logan and Irwin 1985; Jalkotzy et al. 2000). However, many studies have documented pumas utilizing woody vegetation as the primary source of stalking cover (Laing 1988; Logan and Irwin 1985; Koehler et al. 1991; Laundre et al. 2003). The results from this study provide additional evidence that pumas select for areas that have increased stalking cover provided by woody vegetation to ambush prey as woody cover was a covariate in the highest ranking models for all of the datasets except for the Chihuahuan Desert model set, where visibility was a stronger predictor of puma kill sites. In the Chihuahuan Desert, woody cover is more abundant on the landscape, therefore the effect of visibility on puma kill sites was more evident because there were likely similar levels of woody cover at kill sites and random locations. Woody cover was a predictor for puma kills in the Sonoran deserts. This is likely due to there being less woody vegetation within the Sonoran Desert landscape (kill sites: mean 0.225 SD ± 0.259; random location: mean 0.133 SD ± 0.171) when compared to the Chihuahuan Desert (kill sites: mean 0.128 SD ± 0.141; random locations: mean 0.101 SD ± 0.145). Therefore, the effect of woody cover was more evident on puma kills when compared to the random locations in the Sonoran Desert.

Grant et al. (2005) reported that African lions select areas with increased cover where prey are easier to catch. The prevalent relationship between puma kills and woody cover suggest that pumas also select for areas with increased ambush cover in which prey are easier to catch (Pierce et al. 2004; Elbroch et al. 2012). Aside from stalking cover for predators, the shade provided by woody cover is used by predators and prey for thermoregulation and can become a limiting factor to wildlife during hot seasons in arid and semi-arid regions (Rosenstock et al. 1999; Cain et al. 2008b). Though there are many other landscape features that can provide shade for wildlife (i.e., boulders, canyons, northern aspects), ungulate prey may be more attracted to areas with woody cover shade because of the added benefit of foraging opportunities within the woody vegetation.

The models that had woody cover without distance to water did not perform well indicating that woody cover alone does not explain the distribution of puma kills. Some of the African lion studies reported piospheres surrounding waterholes caused by the large concentrations of grazers overutilizing and trampling the vegetation (Tambling et al. 2013) resulting in reduced ambush cover for lions. This might also be true for pumas in the Southwest in areas with substantial livestock grazing (Fusco et al. 1999; Nash et al. 1999; deLeeuw et al. 2001; Brooks et al. 2006). Although ungulate prey densities might be higher at closer proximities to water sources within the piospheres, puma predation might be limited to the peripheral areas that have more cover where puma are more successful in stalking and ambushing prey. Intensive livestock grazing near water sources can also reduce the amount of palatable forage available to ungulate prey within the piospheres (James et al. 1999) and force prey to forage in areas that have increased predation risk to meet nutritional demands (Pierce et al. 2004; DeCesare et al. 2014). Native southwestern wildlife species also aggregate at water sources during dry seasons, but they are not considered to be as detrimental to the habitat as livestock and feral ungulates (Marshal et al. 2006). Therefore, the piosphere effect is not as pronounced in areas without livestock grazing in the Southwest.

Drought severity or average temperature and distance to man-made water were included in most of the highest ranking models for each dataset indicating that aridity strongly influenced the relationships between puma predation sites and distance to water. Climatic conditions likely affected the water requirements of prey and influenced their distribution on the landscape by restricting them to areas near man-made water sources. Prior to the development of man-made wildlife water sources, some ungulate prey species were spatially restricted to the areas near natural occurring water sources during the hot and dry seasons but would utilize areas further from water sources during the wet season (Wright 1959). It was expected that aridity and temperature would influence prey kill proximity to man-made water in the desert areas, however drought severity was also a predictor for kill proximity to man-made water in the non-desert areas that generally have cooler temperatures, receive more precipitation, and have more available natural water sources. This indicates that prey frequent man-made water sources during dry and hot periods even in areas that have increased availability of natural water. Elk were more prevalent in the diets of pumas within the non-desert areas, which might partially explain this result as the water requirements of elk are higher than most of the other ungulates (Rosenstock et al. 1999). Throughout the year, elk have been reported to occur within 0.4 to 1.6 km of water sources and occur within 0.4 to 0.8 km during dryer seasons and lactation (Delguidice et al. 1984; Brown 1994).

Consistent with many previous diet studies, mule deer composed most of the kills in the data (Logan and Sweanor 2001; De La Torre et al. 2009; Villepique et al. 2011; Wilkens et al.

2015), contributing to the similarities in the results for the all study areas and deer kills only model sets. Deer were the most common prey species at all of the study areas except for the Ladder Ranch and Jemez Mountains where elk were most common and deer were the second most common prey. It was expected that the availability of ephemeral water during the wet season would have increased the variability of proximity of kills to water sources compared to the dryer and hotter seasons. However, the increased abundance of deer fawns and elk calves born during the hot-wet season could explain why the models that included season had lower performance. Lactating female ungulates have higher water requirements that might spatially restrict them to water sources even during the wetter seasons (Bleich et al. 1997; Krausman 2002). The habitat selection of GPS-collared pumas and deer in the Gallinas Mountains indicated that pumas mostly selected for canopy cover and slope, whereas deer often selected areas closer to water sources (Kay 2018).

Season was a predictor for bighorn sheep kills, however mere distance to water was a stronger predictor for bighorn kill site locations. Although desert bighorn sheep are well-adapted to survive in arid regions, studies have reported that bighorn sheep are commonly located within 4 km of a man-made water source throughout the year but occur at closer proximities during the hotter and dryer seasons (Wilson 1971; Turner et al. 2004). Our findings provide further evidence that man-made water structures influence bighorn habitat use as the mean distance between bighorn kills and water sources was within 4 km. Predation risk for bighorn sheep increased in the areas surrounding water sources that had more woody cover, specifically during the hotter seasons. In the Southwest, bighorn breed during the hot-wet season when forage is more abundant and bighorn nutritional condition is highest. Lambing season typically occurs from February through May during the last months of the cool-dry season and early parts of the hot-dry season. It is not uncommon for females to be lactating during the hot-dry season, which increases their dependency on water, spatially restricting them to areas near water sources (Bleich et al. 1997; Cain et al. 2006; Cain et al. 2008b; Krausman 2002).

Man-made water sources are often developed in areas that are favorable to livestock and wildlife. Historically, water wells were dug in areas where the water table was closest to the ground surface which typically have more vegetative heterogeneity compared to areas where the water table is further from the ground surface. Habitats surrounding man-modified springs typically have higher quality forage compared to the surrounding areas. The locations of rain catchments (i.e., guzzlers, retention dams, sand tanks) are often selected by game managers for habitat features such as available forage, proximity to escape terrain (Whitting et al. 20011), and the effectiveness of the surface to catch precipitation or support a guzzler structure (Simpson et al. 2011). Tinajas, or rock tanks that pool water for extended periods after precipitation events, are typically naturally occurring but have been modified by man-made structures that enhance their storage capacity and or reduce evaporation. Therefore, some of the puma kills may have occurred at locations proximate to man-made water sources regardless of the availability of water because of other preferred habitat features within those areas.

In the arid regions of the southwestern United States, pumas do not appear to be exploiting the predictable prey visitation of man-made water sources but assuming that the concentrated distribution of prey species within 3 – 5 km of water sources corresponds to increased prey density, it does appear that puma are capitalizing on the increased densities of prey in the vicinities of water. On a home range scale, puma select areas proximate to water sources that have increased prey abundance and higher probabilities of encountering prey for hunting. Within the home range, pumas select fine scale habitat features, such as woody cover, that enhance their ability to stalk, ambush, and effectively kill prey. Climatic conditions, such as drought severity and average temperature influence the distribution of prey species on the landscape by restricting them to areas closer to man-made water sources during dryer and hotter periods. Therefore, puma kill site locations occur at closer proximities to man-made water sources during the hotter and dryer seasons, even in areas that are less arid and have increased availability of alternate water sources.

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Table 3: Prey kill data collected from GPS collared lions in Arizona and New Mexico from 2007 – 2018.

Study Area	Study Area Size based on 90% Cummulative KDE of Puma GPS Fixes (km²)	Number of Collared Pumas			Number of Prey Kills per Species										Kills per Season			Number of Manmade Water Sources Within Area
		Male	Female	Total Pumas	Barbary Sheep	Bighorn	Elk	Feral Burro	Feral Horse	Javelina	Mule Deer	Gemsbok	Pronghorn	Total Kills	Cool-Dry	Hot-Dry	Hot-Wet	
Arizona	8,318	11	10	21		28		18		104	333			483	292	99	92	271
Armendaris	3,825	7	1	8		21	2			4	76	35	6	144	56	16	72	168
Gallinas	1,060	2	1	3	3		23				95			121	23	23	75	43
Jemez	2,987	7	5	12			156				69			225	75	43	107	291
Kofa	11,177	12	11	23		95			6	3	155			259	132	95	32	131
Ladder	2,731	9	3	12			101			24	96		4	225	97	65	63	318
Sevilleta	3,604		3	3		1	5				77		16	99	39	7	53	54
Total	33,702	48	34	82	3	145	287	18	6	135	901	35	26	1556	714	348	494	1276

Table 2: Model number and structure of a priori models used to examine the influence of man-made water sources on puma kill site distribution in the Chihuahuan and Sonoran deserts from 2007 – 2018. Models were replicated for each of the seven data subsets: combined study areas, Sonoran Desert areas, Chihuahuan Desert areas, desert study areas, non-desert areas, only deer kills, and only bighorn kills. Models that included Prey Species were not used for the only deer kills and only bighorn kills subsets.

Model Structure[1]	**Model Set**[2]
Water + Season + Water x Season	A
Water + PDSI + Water x PDSI	A
Water + TAVG + Water x TAVG	A
Water + Woody + Water x Woody	A
Water + Visibility + Water x Visibility	A
Water + VRM + Water x VRM	A
Water + EVT + Water x EVT	A
Water + Study Area + Water x Study Area	A
Water	A
Water + Prey Species + Water x Prey Species	B
Water + Season	A
Water + PDSI	A
Water + TAVG	A
Water + Woody	A
Water + Visibility	A
Water + VRM	A
Water + EVT	A
Water + Study Area	A
Water + PDSI + Woody + Water x PDSI x Woody	A
Water + Prey Species	B
Water + TAVG + Woody + Water x TAVG x Woody	A
Woody + Season + Woody x Season	A
Woody + PDSI + Woody x PDSI	A
Woody + TAVG + Woody x TAVG	A
Woody + Visibility + Woody x Visibility	A
Woody + VRM + Woody x VRM	A
Woody + Study Area + Woody x Study Area	A
Woody	A
Woody + Prey Species + Woody x Prey Species	B
Water + PDSI + Study Area + Water x PDSI x Study Area	A
Water + Season + Study Area + Water x Season x Study Area	A

[1] Variable notation: Water = distance to nearest man-made water sources; Season = hot-dry (HD), cool-dry (CD), or hot-wet (HW); Woody = amount of woody cover; VRM = terrain ruggedness;

PDSI = Palmer drought severity index; TAVG = average temperature; EVT = estimated vegetative type; Visibility = amount of visible area.

[2] A = model included in all model sets, B = model included in all model sets except set that evaluated only deer kills.

Table 4: The eight highest ranking models for each of the data subsets. Kill site data collected from GPS-collared pumas in Arizona and New Mexico from 2007 – 2018.

Data	Model	K	logLik	AICc	ΔAICc	AICc Weight	Deviance
Ungulate Kills at All Study Areas	Water + PDSI + Woody + Water x PDSI x Woody	9	-6119.702	12257.409	0.000	0.995	12239.4
	Water + TAVG + Woody + Water x TAVG x Woody	9	-6125.101	12268.207	10.798	0.005	12250.2
	Water + Woody + Water x Woody	5	-6137.182	12284.365	26.957	0.000	12274.4
	Woody + Visibility + Woody x Visibility	5	-6165.994	12341.989	84.581	0.000	12332
	Water + Study Area + Water x Study Area	15	-6159.318	12348.650	91.242	0.000	12318.6
	Woody + Study Area + Woody x Study Area	15	-6165.472	12360.960	103.551	0.000	12330.9
	Water + PDSI + Study Area + Water x PDSI x Study Area	29	-6153.440	12364.932	107.524	0.000	12306.9
	Water + Woody	4	-6181.927	12371.855	114.446	0.000	12363.9
Ungulate Kills in the Sonoran Desert Study Areas	Water + Woody + Water x Woody	5	-1423.144	2856.296	0.000	0.422	2846.3
	Water + Woody	4	-1424.498	2857.002	0.705	0.297	2839.4
	Water + TAVG + Woody + Water x TAVG x Woody	9	-1419.696	2857.416	1.119	0.241	2843
	Water + PDSI + Woody + Water x PDSI x Woody	9	-1421.494	2861.011	4.715	0.040	2944.8
	Woody + Study Area + Woody x Study Area	5	-1442.543	2895.093	38.797	0.000	2884
	Woody + Season + Woody x Season	7	-1441.997	2898.008	41.712	0.000	2888.7
	Woody + Visibility + Woody x Visibility	5	-1444.329	2898.665	42.368	0.000	2892.8
	Woody	3	-1446.378	2898.759	42.463	0.000	2891.3
Ungulate Kills in the Chihuahuan Desert Study Areas	Water + Visibility + Water x Visibility	5	-600.554	1211.126	0.000	0.997	1201.1
	Water + Study Area + Water x Study Area	7	-604.714	1223.461	12.336	0.002	1209.4
	Woody + Visibility + Woody x Visibility	5	-609.431	1228.880	17.754	0.000	1218.9
	Woody + TAVG + Woody x TAVG	5	-609.960	1229.939	18.813	0.000	1219.9
	Water + Woody	4	-611.187	1230.387	19.261	0.000	1222.4

	Water + Vegetation + Water x Vegetation	9	-606.304	1230.663	19.537	0.000	1212.6
	Water + Study Area	5	-610.430	1230.879	19.753	0.000	1220.9
	Water + Vegetation	6	-609.748	1231.522	20.396	0.000	1219.5
Ungulate Kills in the Non-desert Study Areas	Water + Woody + Water x Woody	5	-686.870	1383.756	0.000	0.589	1373.7
	Water + PDSI + Woody + Water x PDSI x Woody	9	-683.621	1385.291	1.535	0.273	1367.2
	Water + TAVG + Woody + Water x TAVG x Woody	9	-685.221	1388.492	4.736	0.055	1370.4
	Water + Woody	4	-691.119	1390.249	6.493	0.023	1382.2
	Water + Visibility	5	-690.431	1390.878	7.122	0.017	1380.9
	Water + Ruggedness	5	-690.524	1391.065	7.309	0.015	1381
	Woody	3	-693.126	1392.259	8.503	0.008	1386.3
	Water + Vegetation + Water x Vegetation	9	-688.063	1394.176	10.420	0.003	1376.1
Ungulate Kills in the Desert Study Areas	Water + Woody + Water x Woody	5	-941.038	1892.088	0.000	0.647	1882.1
	Water + TAVG + Woody + Water x TAVG x Woody	9	-938.143	1894.321	2.234	0.212	1876.3
	Water + PDSI + Woody + Water x PDSI x Woody	9	-938.547	1895.129	3.041	0.141	1877.1
	Woody + Visibility + Woody x Visibility	5	-951.215	1912.441	20.354	0.000	1902.4
	Water + Study Area + Water x Study Area	11	-950.420	1922.891	30.804	0.000	1900.8
	Woody + TAVG + Woody x TAVG	5	-957.219	1924.449	32.361	0.000	1914.4
	Woody	3	-959.452	1924.909	32.821	0.000	1918.9
	Water + Vegetation	6	-957.267	1926.551	34.463	0.000	1914.5
Deer Kills at All Study Areas	Water + PDSI + Woody + Water x PDSI x Woody	9	-3529.750	7077.509	0.000	0.998	7059.5
	Water + Woody + Water x Woody	5	-3540.708	7091.418	13.909	0.001	7081.4
	Water + TAVG + Woody + Water x TAVG x Woody	9	-3537.288	7092.586	15.077	0.001	7074.6
	Woody + Visibility + Woody x Visibility	5	-3543.291	7096.586	19.077	0.000	7086.6
	Water + Woody	4	-3560.090	7128.182	50.673	0.000	7120.2

	Water + Study Area + Woody + Water x Study Area x Woody	15	-3554.414	7138.854	61.345	0.000	7108.8
	Woody + Visibility + Woody x Visibility	5	-3568.201	7146.406	68.897	0.000	7136.4
	Natural Water + PDSI + Woody + Natural Water x PDSI x Woody	9	-3575.624	7169.258	91.749	0.000	7151.2
Bighorn Kills at Study Areas With Bighorn Populations	Water	3	-134.807	275.646	0.000	0.142	269.6
	Water + Season + Water x Season	7	-130.907	275.962	0.316	0.121	261.8
	Water + TAVG + Woody + Water x TAVG x Woody	9	-128.901	276.041	0.395	0.117	257.8
	Water + Woody + Water x Woody	5	-133.202	276.484	0.838	0.094	266.4
	Water + Visibility	4	-134.399	276.851	1.205	0.078	268.8
	Water + Woody	4	-134.649	277.352	1.706	0.061	269.3
	Water + Ruggedness	4	-134.719	277.490	1.844	0.057	269.4
	Water + TAVG	4	-134.719	277.491	1.845	0.057	269.4

Table 5: Standardized parameter estimates from the top ranking mixed-effects regression models for puma kill site locations in Arizona and New Mexico from 2007 - 2018.

Data	Model Variable	Estimate	*SE*	Adjusted *SE*	*Z* Value	Pr (>|Z|)
Ungulate Kills at All Study Areas	Water	-0.3971	0.0421	0.0421	9.439	< 0.001
	PDSI	0.0247	0.0307	0.0307	0.804	0.421
	Woody	0.3101	0.0292	0.0292	10.634	< 0.001
	Water x PDSI	0.1169	0.0358	0.0358	3.265	0.001
	Water x Woody	0.2272	0.0280	0.0280	8.114	< 0.001
	PDSI x Woody	-0.0165	0.0220	0.0220	0.75	0.453
	Water x PDSI x Woody	0.0719	0.0264	0.0264	2.725	0.006
Ungulate Kills in the Sonoran Desert Study Areas	Water	-0.4245	0.0831	0.0831	5.107	< 0.001
	Woody	0.5433	0.0588	0.0588	9.241	< 0.001
	Water x Woody	0.0676	0.0613	0.0613	1.102	0.27
	TAVG	-0.0749	0.0729	0.0729	1.027	0.304
	Water x TAVG x Woody	0.1155	0.0698	0.0698	1.655	0.098
Ungulate Kills in the Chihuahuan Desert Study Areas	Water	-0.6513	0.2068	0.2069	3.148	0.002
	Visibility	-0.4497	0.1265	0.1265	3.554	< 0.001
	Water x Visibility	0.0902	0.1573	0.1574	0.573	0.567
Ungulate Kills in the Non-desert Study Areas	Water	-0.0741	0.1702	0.1702	0.435	0.663
	Woody	0.2478	0.0862	0.0863	2.873	0.004
	Water x Woody	0.2022	0.0967	0.0968	2.089	0.037
	PDSI	0.0563	0.1163	0.1163	0.484	0.629
	Water x PDSI x Woody	0.0485	0.0833	0.0834	0.581	0.56
Ungulate Kills in the Desert Study Areas	Water	-0.5325	0.1028	0.1028	5.179	< 0.001
	Woody	0.4860	0.0776	0.0776	6.264	< 0.001
	Water x Woody	0.1402	0.0821	0.0822	1.706	0.088
	TAVG	-0.0220	0.0820	0.0820	0.269	0.788
	Water x TAVG	-0.1226	0.1054	0.1055	1.163	0.245

	TAVG x Woody	0.1886	0.0831	0.0832	2.268	0.023
	Water x TAVG x Woody	0.0802	0.0908	0.0909	0.883	0.377
	PDSI	0.0175	0.0836	0.0836	0.209	0.835
	Water x PDSI	0.1347	0.1091	0.1091	1.235	0.217
	PDSI x Woody	0.0047	0.0835	0.0836	0.056	0.956
	Water x PDSI x Woody	0.2212	0.1201	0.1201	1.841	0.066
Deer Kills at All Study Areas	Water	-0.3989	0.0514	0.0514	7.755	< 0.001
	PDSI	0.0475	0.0385	0.0385	1.235	0.217
	Woody	0.3605	0.0368	0.0368	9.786	< 0.001
	Water x PDSI	0.1535	0.0433	0.0433	3.542	< 0.001
	Water x Woody	0.1999	0.0339	0.0339	5.892	< 0.001
	PDSI x Woody	-0.0098	0.0299	0.0299	0.33	0.741
	Water x PDSI x Woody	0.0492	0.0349	0.0349	1.41	0.157
Bighorn Kills at Study Areas With Bighorn Populations	Water	-1.8477	0.7306	0.7310	2.527	0.012
	Season=CD	1.0087	0.8188	0.8197	1.23	0.219
	Season=HW	0.9496	0.8772	0.8783	1.081	0.279
	Water x Season=CD	2.323	0.9586	0.9601	2.419	0.016
	Water x Season=HW	2.4019	1.1122	1.114	2.156	0.031
	TAVG	-0.3300	0.3714	0.3718	0.888	0.375
	Woody	0.1176	0.3358	0.3362	0.35	0.727
	Water x TAVG	-0.5569	0.5167	0.5175	1.076	0.282
	Water x Woody	0.2978	0.5346	0.5352	0.556	0.578
	TAVG x Woody	0.8133	0.3261	0.3266	2.49	0.013
	Water x TAVG x Woody	0.9397	0.4989	0.4997	1.881	0.06

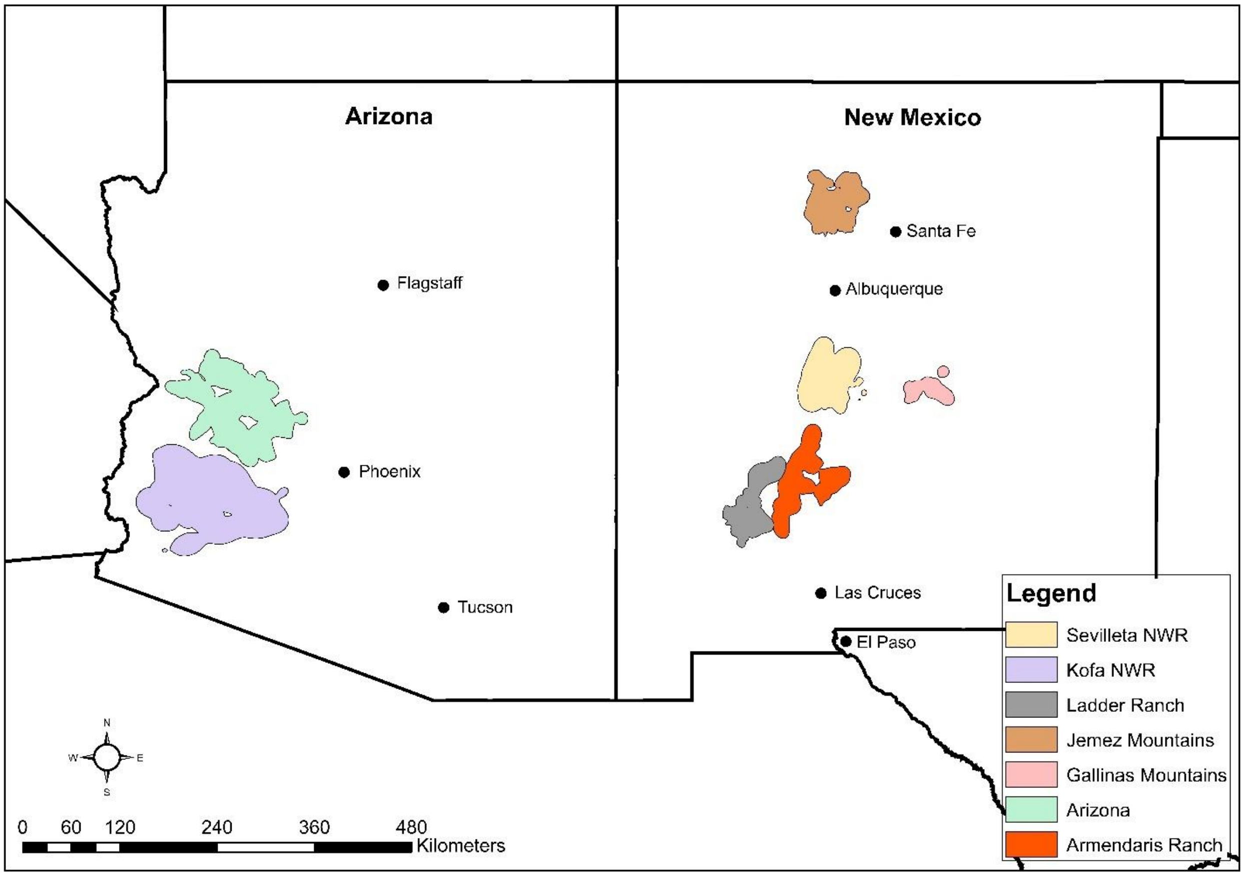

Figure 2. Location of the study areas from which kill data was collected from satellite collared pumas in Arizona and New Mexico from 2007 – 2018. The polygons represent the cumulative 90% KDE home range of the GPS fixes acquired by all of the collared pumas at each study area.

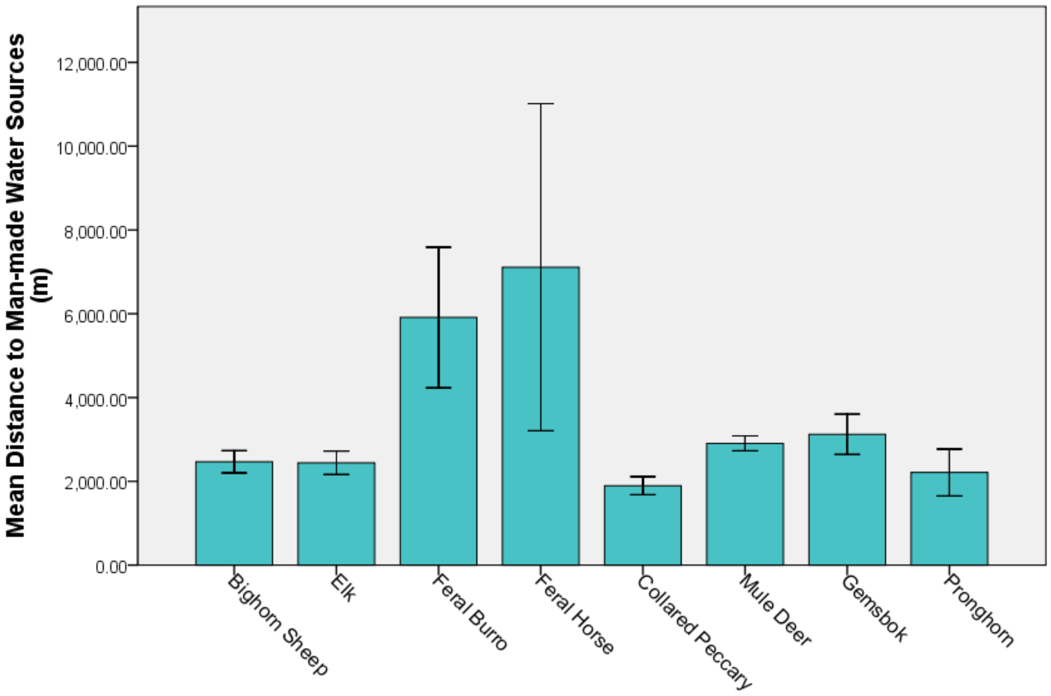

Figure 3. The mean distance (m) of puma prey kills to man-made water sources in Arizona and New Mexico. Data was collected from satellite-collared pumas from 2007 – 2018. The error bars represent the 95% confidence intervals.

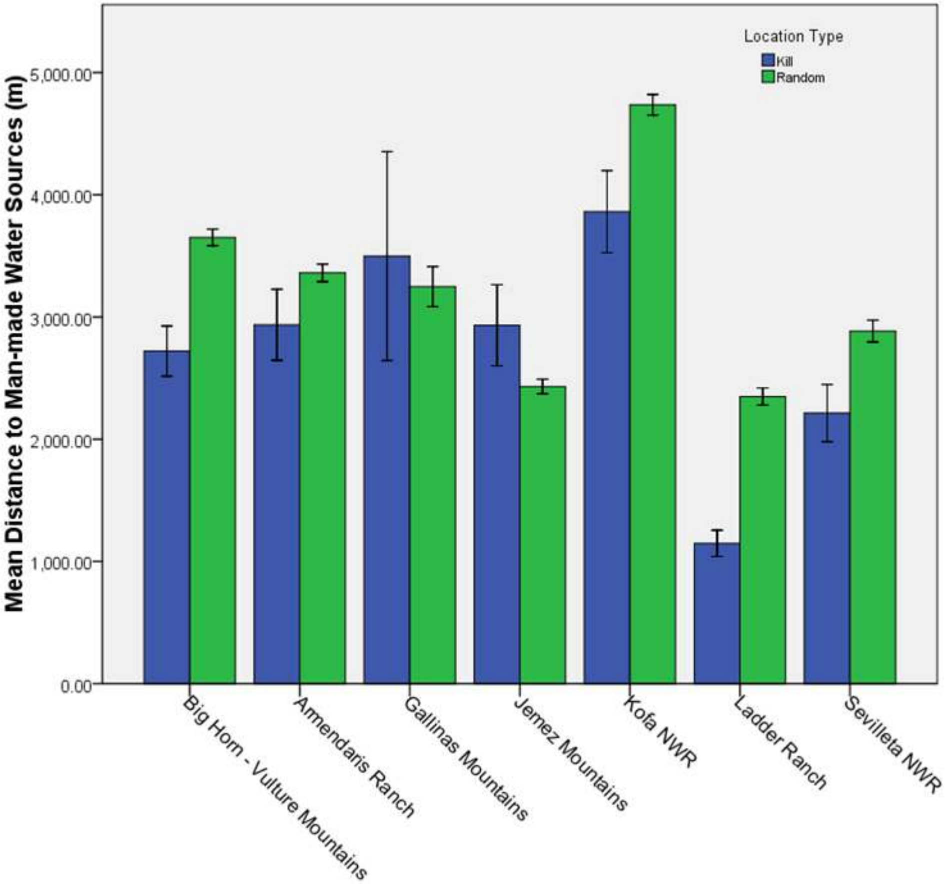

Figure 4.. The mean distances (m) of satellite-collared puma kill sites and random locations to manmade water sources at each study area in New Mexico and Arizona from 2007 – 2018.The error bars represent the 95% confidence intervals.

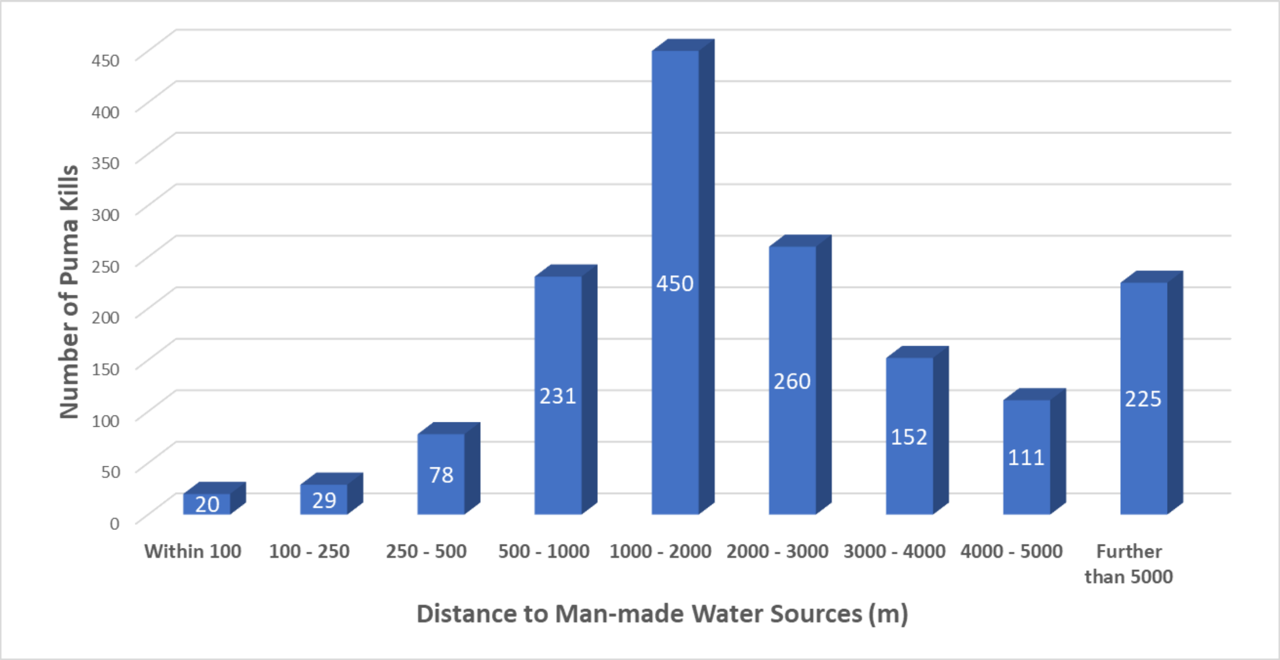

Figure 5. The number of puma prey kills within different proximities to man-made water sources. Data collected from satellite collared pumas in Arizona and New Mexico from 2007 – 2018.

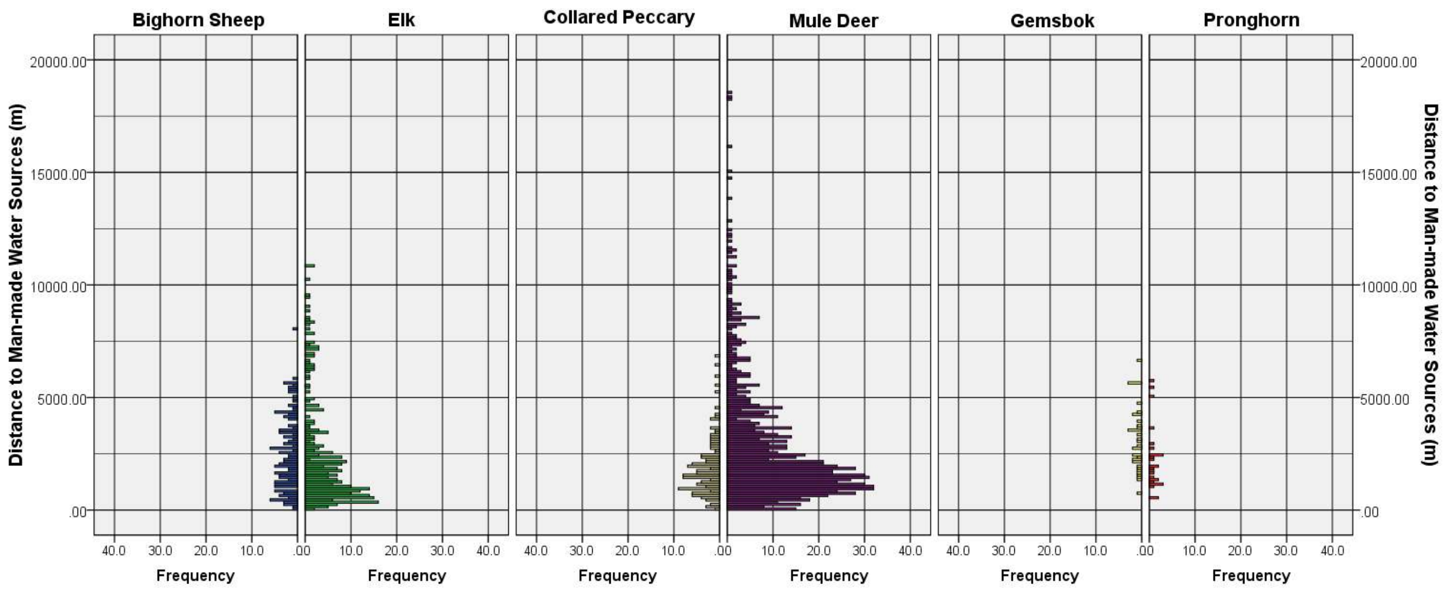

Figure 6. The frequency of common puma prey kills proximate to manmade water sources at 100 m incremented distances. Data collected from satellite-collared pumas in Arizona and New Mexico from 2007 – 2018.

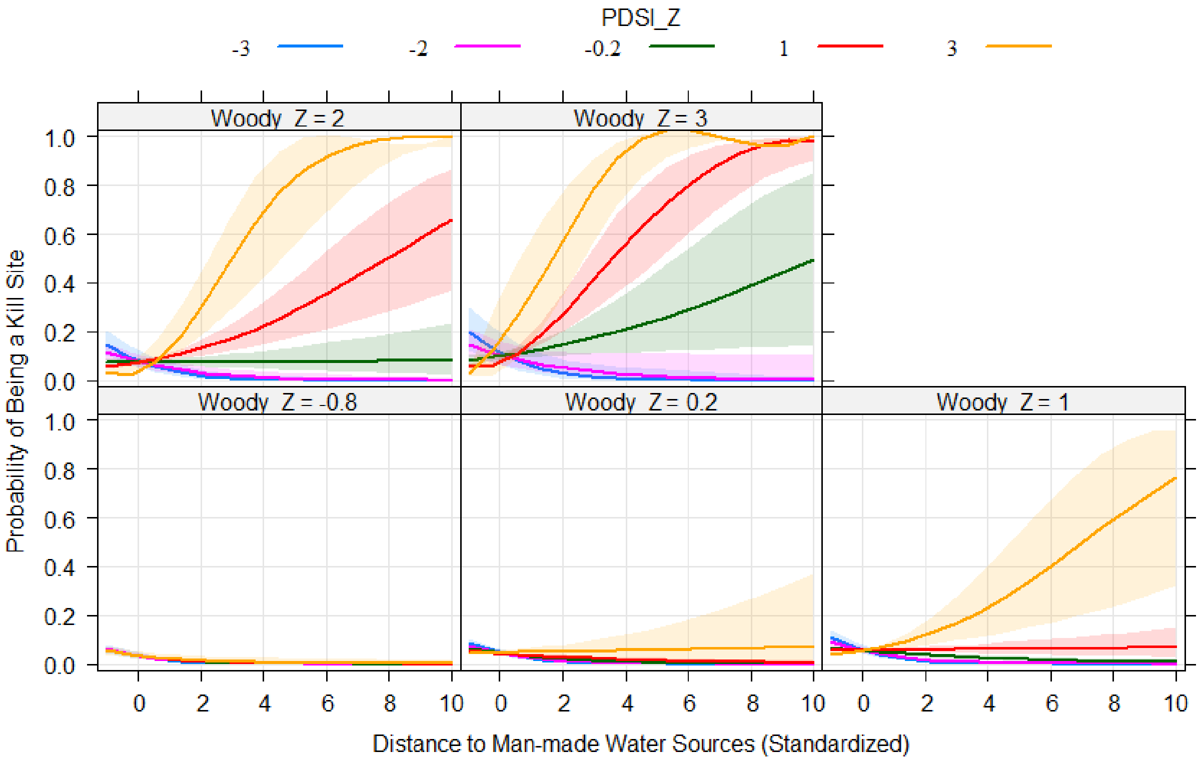

Figure 7. Top-ranking model for puma prey kills at all study areas in Arizona and New Mexico from 2007 – 2018. Plot shows the effects of PDSI and woody cover on the probability of a location being a puma kill relative to manmade water sources (Distance to man-made water source x PDSI x Woody Cover).

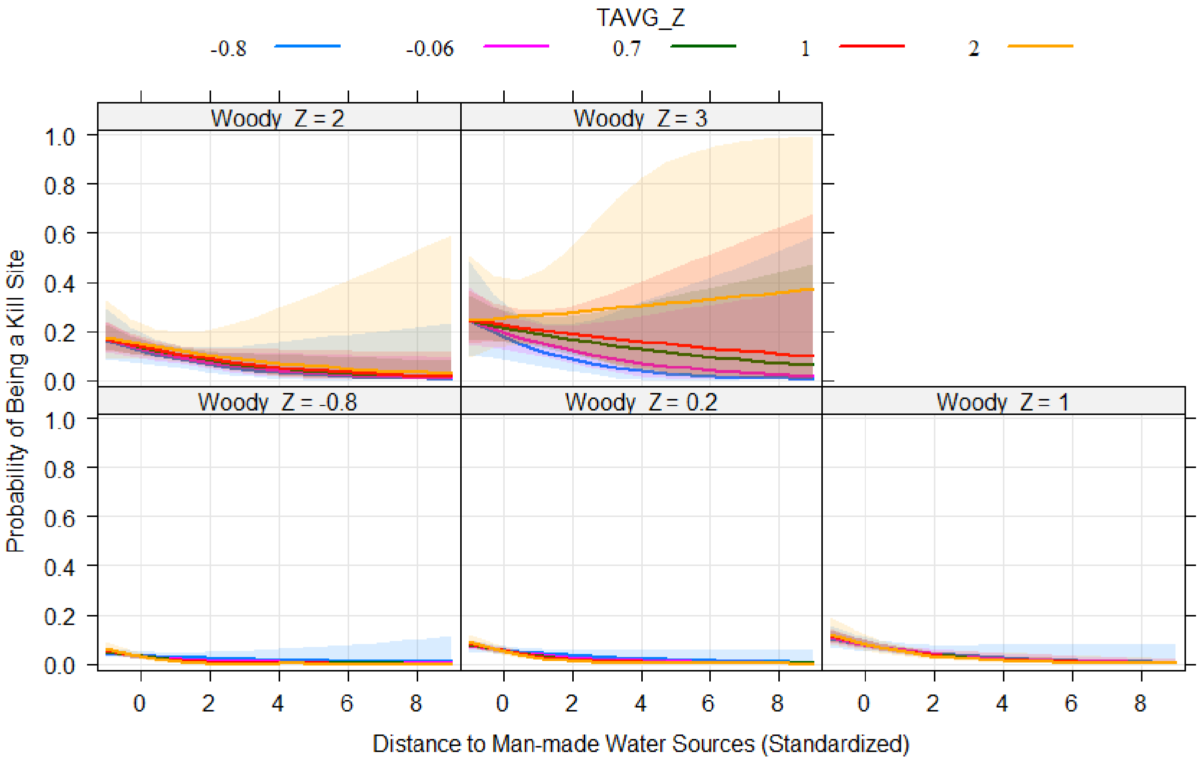

Figure 8: Highest ranking model for puma kill sites in the Sonoran Desert, Arizona from 2007 – 2018. Plot shows the effects of distance to man-made water, average temperature, and woody cover on the probability of a location being a puma kill in the Sonoran Desert (distance to man-made water x TAVG x woody cover).

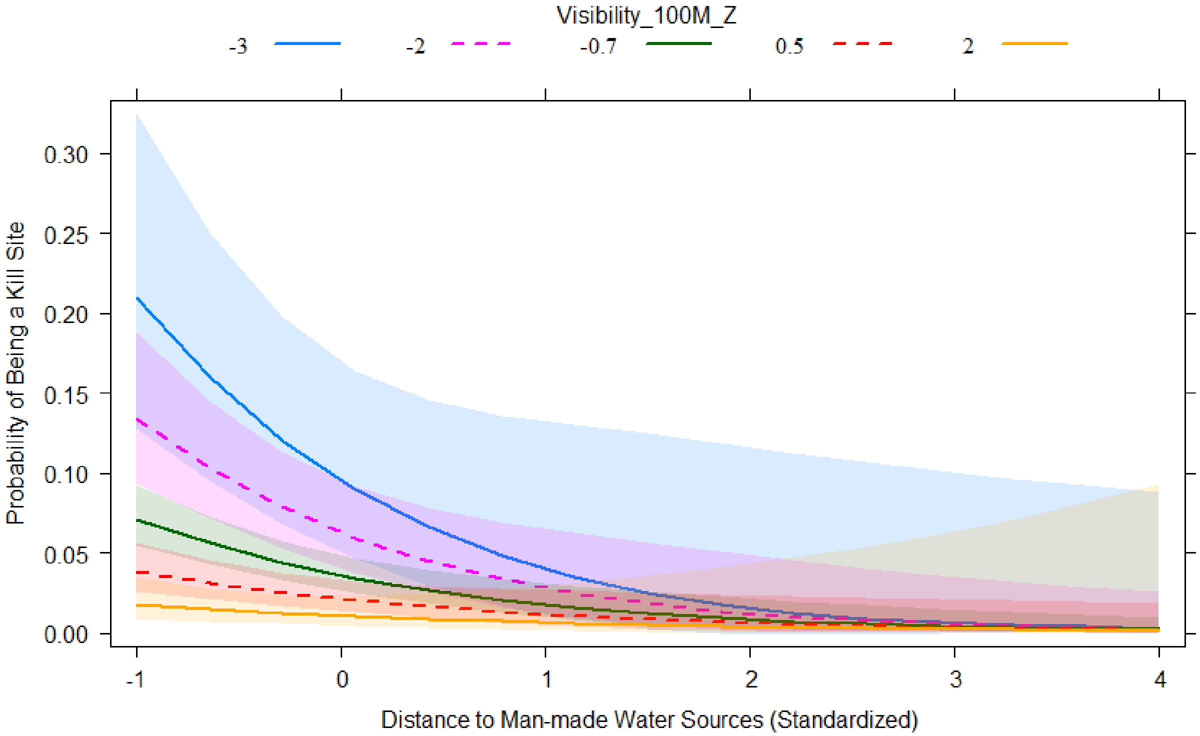

Figure 9. Highest ranking model for puma kill sites in the Chihuahuan Desert, New Mexico from 2007 – 2018. Plot shows the effects of distance to man-made water and visibility on the probability of a location being a puma kill in the Chihuahuan Desert (distance to man-made water x visibility).

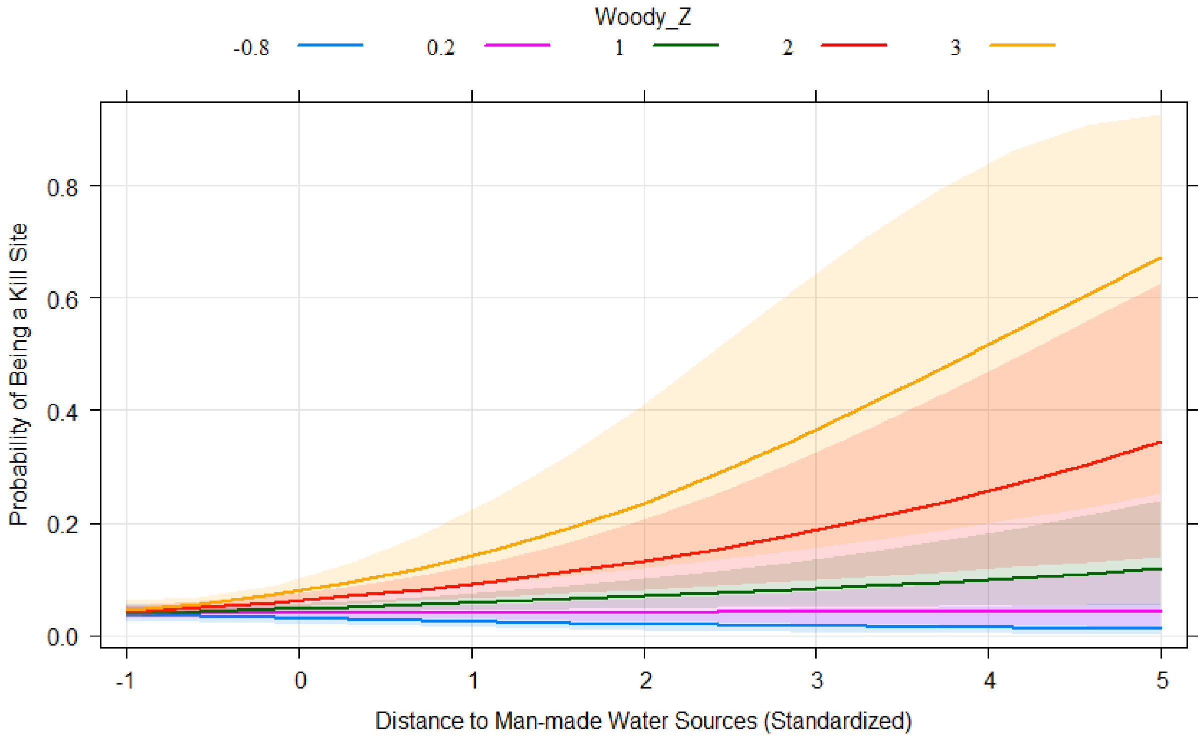

Figure 10. Highest ranking model for puma kill sites in the two non-desert study areas in northern New Mexico from 2007 – 2018. Plot shows the effects of distance to man-made water sources and woody cover on the probability of a location being a kill site (distance to man-made water x woody cover).

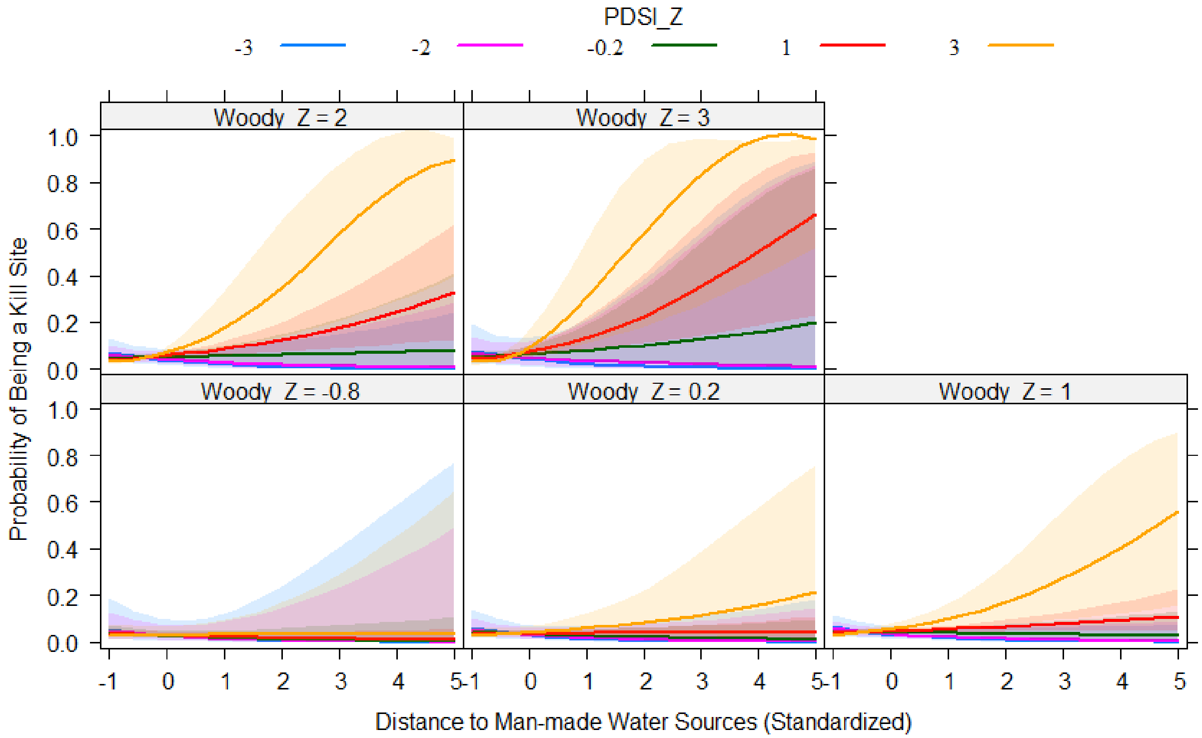

Figure 11. Second highest ranking model for puma kill sites in the two non-desert study areas in northern New Mexico from 2007 – 2018. Plot shows the effects of distance to man-made water sources, drought, and woody cover on the probability of a location being a kill site (distance to man-made water x PDSI x woody cover).

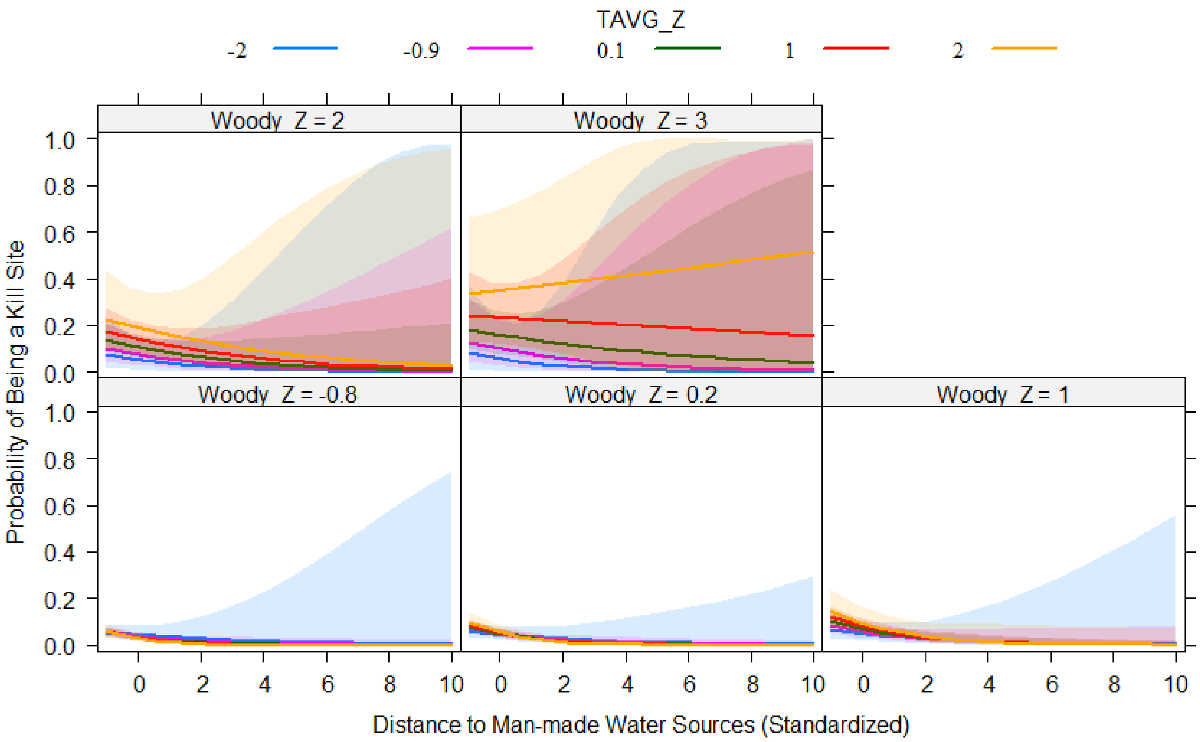

Figure 12. Second highest ranking model for puma kill sites in the combined Sonoran and Chihuahuan desert study areas in southwestern Arizona and New Mexico from 2007 – 2018. Plot shows the effects of distance to man-made water sources, average temperature, and woody cover on the probability of a location being a kill site (distance to man-made water x TAVG x woody cover).

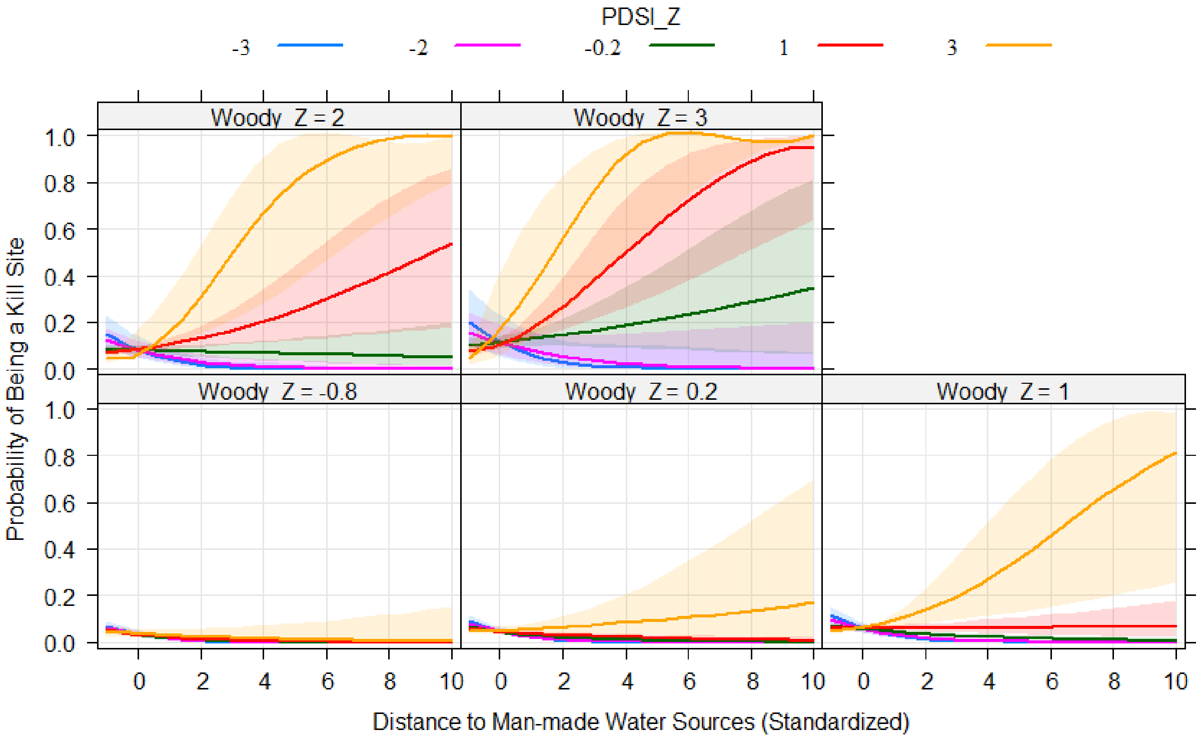

Figure 13. The highest ranking model for deer kill sites made by pumas in the combined study areas in southwestern Arizona and New Mexico from 2007 – 2018. Plot shows the effects of distance to man-made water sources, drought, and woody cover on the probability of a location being a deer kill site (distance to man-made water x PDSI x woody cover).

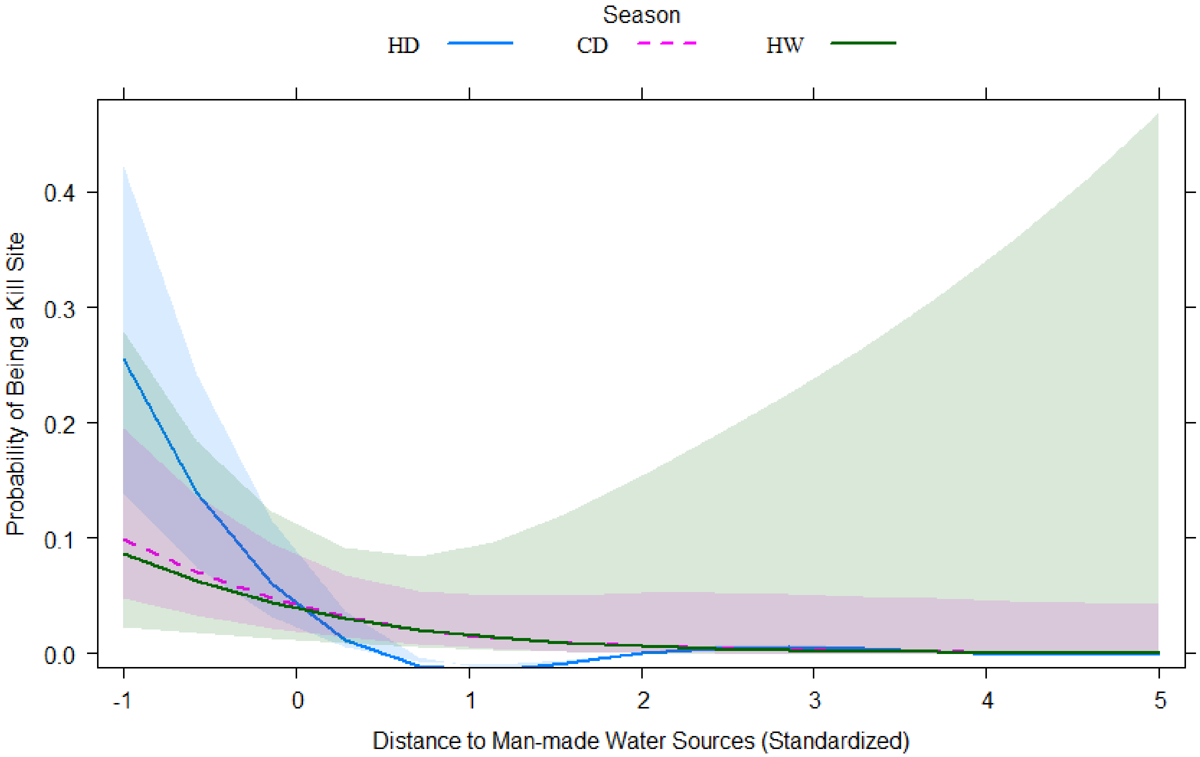

Figure 14. The highest ranking model for bighorn kill sites made by pumas in the study areas with bighorn sheep populations in southwestern Arizona and New Mexico from 2007 to 2018. Plot shows the effects of distance to man-made water sources and season on the probability of a location being a bighorn kill site (distance to man-made water x season).