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Authors: Prude, Charles H., and Cain, James W.

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Habitat diversity influences puma *Puma concolor* diet in the Chihuahuan Desert

Charles H. Prude and James W. Cain III

C. H. Prude, New Mexico Cooperative Fish and Wildlife Research Unit, Dept of Fish Wildlife and Conservation Ecology, New Mexico State Univ., Las Cruces, NM, USA and Turner Biodiversity, Turner Enterprises Inc., Engle, NM, USA. – J. W. Cain III (<https://orcid.org/0000-0003-4743-516X>) ✉ (jwcain@nmsu.edu), U.S. Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, Dept of Fish Wildlife and Conservation Ecology, New Mexico State Univ., Las Cruces, NM, USA.

Habitat heterogeneity and corresponding diversity in potential prey species should increase the diet breadth of generalist predators. Many previous studies describing puma *Puma concolor* diets in the arid regions of the southwestern United States were focused within largely xeric locations, overlooking the influence of heterogeneity created by riparian forests. Such habitat heterogeneity and corresponding prey diversity could influence prey availability and puma diet composition. We examined seasonal prey composition of pumas occupying areas with different habitat conditions representing riparian areas adjacent to the Rio Grande and xeric Chihuahuan Desert uplands in southern New Mexico. We collected prey composition data from 686 kill sites made by 17 (9 males and 8 females) GPS-collared pumas from 2014 to 2018. Diet composition included 32 different avian, aquatic, small mammal, and ungulate prey species. Prey composition varied, with more ungulate prey 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. Prey composition also varied between puma sex and habitat 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 landscapes in southern New Mexico provide additional evidence that pumas have broad diets that are strongly influenced by the habitat and prey community that their home range encompasses.

Key words: diet composition, habitat heterogeneity, mountain lion, New Mexico, prey diversity, puma, *Puma concolor*

Animal behavior, primary productivity, and other environmental conditions influence the abundance, distribution, and vulnerability of prey species (Luttbeg et al. 2003). Areas with heterogeneous habitat conditions often have higher prey abundance when compared to more homogeneous habitats (Kerr and Packer 1997). Heterogeneity in habitat conditions affects habitat use and diet for both predators and prey (Hebblewhite et al. 2005, Gorini et al. 2012). Prey often benefit from habitat heterogeneity because the increased diversity in forage can enhance their ability to meet seasonal nutritional and energetic demands compared to homogenous habitats. Additionally, heterogeneous habitats may reduce predation risk, as prey can select areas with conditions that impede foraging by predators (Warfe and Barmuta 2004, Lecomte et al. 2008). Prey can also exploit habitat heterogeneity to mitigate predation risk from multiple predators. For example, elk

Cervus elaphus can select areas with more rugged terrain and dense vegetation to evade cursorial predators (e.g. wolves; *Canis lupus*) or use areas with less vegetation cover and with higher visibility to evade stalking and ambush predators (e.g. puma; *Puma concolor*) (Kohl et al. 2019). On the other hand, predators can benefit from habitat heterogeneity because of the increased diversity, abundance, and in certain conditions also vulnerability of prey (Schooley et al. 1996, Bhattarai and Kindlmann 2012).

Puma is 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 and Merchant 2005, Elbroch and Wittmer 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 deserts in North and South America (Franklin et al 1999, Logan and Sweanor 2001, Choate et al. 2018). Puma morphology, physiology and behavior allow them to thrive in widely varying environmental conditions (Logan and Sweanor 2001).

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The generalist diets and adaptability to various environmental conditions allow pumas to exploit the diversity of prey within heterogeneous landscapes (Tattersall et al. 2002). This is especially true in areas where habitat heterogeneity increases the amount of stalking cover that enhances the ability of pumas to ambush prey (Lehman et al. 2017, Smith et al. 2019).

Pumas prey opportunistically on the most abundant and assailable species across their distribution range (Anderson 1983, Logan and Sweanor 2001), and consume a variety of prey species ranging in size from beetles (likely in association with larger prey items; *Chrysomelidae* spp., Cushman 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 commonly prey on 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, the most common prey are the white-tailed deer *Odocoileus virginianus*, collared peccary *Pecari tajacu*, coatimundi *Nasua narica*, nine-banded armadillo *Dasypos novemcinctus*, and various lagomorph species (*Lepus* spp., *Sylvilagus audubonii*; Nunez et al. 2000, de la Torre and de la Riva 2009). Pumas in North America frequently kill large ungulates such as deer *Odocoileus* spp., elk *Cervus elaphus*, pronghorn *Antilocapra americana* and bighorn sheep *Ovis canadensis*, and a variety of smaller mammals such as beaver *Castor canadensis*, coyote *Canis latrans*, raccoon *Procyon lotor* and skunk *Mephitidae* spp. Although the extent of livestock depredation by puma varies widely across their distribution range, cattle *Bos taurus*, sheep *Ovis aries* and goats *Capra aegagrus*, are also depredated by puma throughout the Americas in areas with ranching and agriculture (Polisar et al. 2003, Rominger et al. 2004). Despite having an extremely diverse diet, many studies have reported deer to be the preferred prey of pumas across different ecoregions (Iriarte et al. 1990, de la Torre and de la Riva 2009, Villepique et al. 2011), comprising, in many cases, more than 50% of consumed prey (Logan and Sweanor 2001, Wilckens et al. 2015).

Previous studies on puma diets in the arid regions of the southwestern United States primarily occurred in areas where the landscape is dominated by upland desert (Cunningham et al. 1999, Logan and Sweanor 2001, Choate et al. 2018). We sought to determine seasonal variation in prey composition and quantify differences in prey composition of pumas occupying the two habitat types including the mesic riparian bosque along the Rio Grande and xeric uplands. To assess the relationship between habitat heterogeneity and puma diet composition, we conducted a four-year study (2014–2018) examining puma diet through field investigation of kill sites at two study areas in the Chihuahuan Desert adjacent to the Rio Grande in south-central New Mexico. We predicted that this heterogeneity in vegetation would result in increased prey diversity and puma diet composition.

Material and methods

Study area

We conducted this study on the Armendaris Ranch (AR) and Sevilleta National Wildlife Refuge (SNWR) in south-central New Mexico (Fig. 1). The AR 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, and Elephant Butte Reservoir to the west. Elevation ranges from 1340 m along the Rio Grande to 2083 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 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 cottonwood *Populus wislizeni*, desert willow *Chilopsis linearis*, willow *Salix exigua* and non-native salt cedar *Tamarix ramosissima* and Russian olive *Elaeagnus angustifolia*. Mean annual precipitation is 23.7 cm (SD \pm 7.6) and mean annual snowfall is 8.6 cm (SD \pm 15.5). Temperatures range from an average daily minimum of 5.3°C (SD \pm 3.1) in January to an average daily maximum 30.6°C (SD \pm 2.3) in July (climate data from Elephant Butte Dam, Truth or Consequences, NM, 1908–2019; WRCC 2018a).

Ungulates common in the xeric uplands on the AR include mule deer *O. hemionus*, pronghorn, non-native gemsbok *Oryx gazella*, and collared peccary. In addition, desert bighorn sheep *O. c. mexicana* occupy the Fra Cristobal Mountains. Potential prey species inhabiting the riparian areas adjacent to the Rio Grande include beaver, raccoon, Rio Grande wild turkey *Meleagris gallopavo intermedia*, and various aquatic species such as spiny softshell turtle *Apalone spinifera* and non-native common carp *Cyprinus carpio*. Other predators or potential scavengers of puma prey kills on the AR include coyote, bobcat *Lynx rufus*, gray fox *Urocyon cinereoargenteus*, golden eagle *Aquila chrysaetos*, and transient black bears *Ursus americanus*. The bosque bordering Elephant Butte Reservoir and the Rio Grande also provide habitat for migratory waterfowl in winter, which increases potential prey at that time (Kelly and Finch 1999).

The SNWR, located 30 km north of Socorro, New Mexico, is a 93 077 ha wildlife refuge managed by US Fish and Wildlife Service. The SNWR is approximately 75 km north of the AR (Fig. 1). The landscape at the SNWR is comparable to the AR and comprises xeric upland desert areas and riparian bosque bordering the Rio Grande. Elevation ranges from 1432 m along the Rio Grande to 2529 m in the

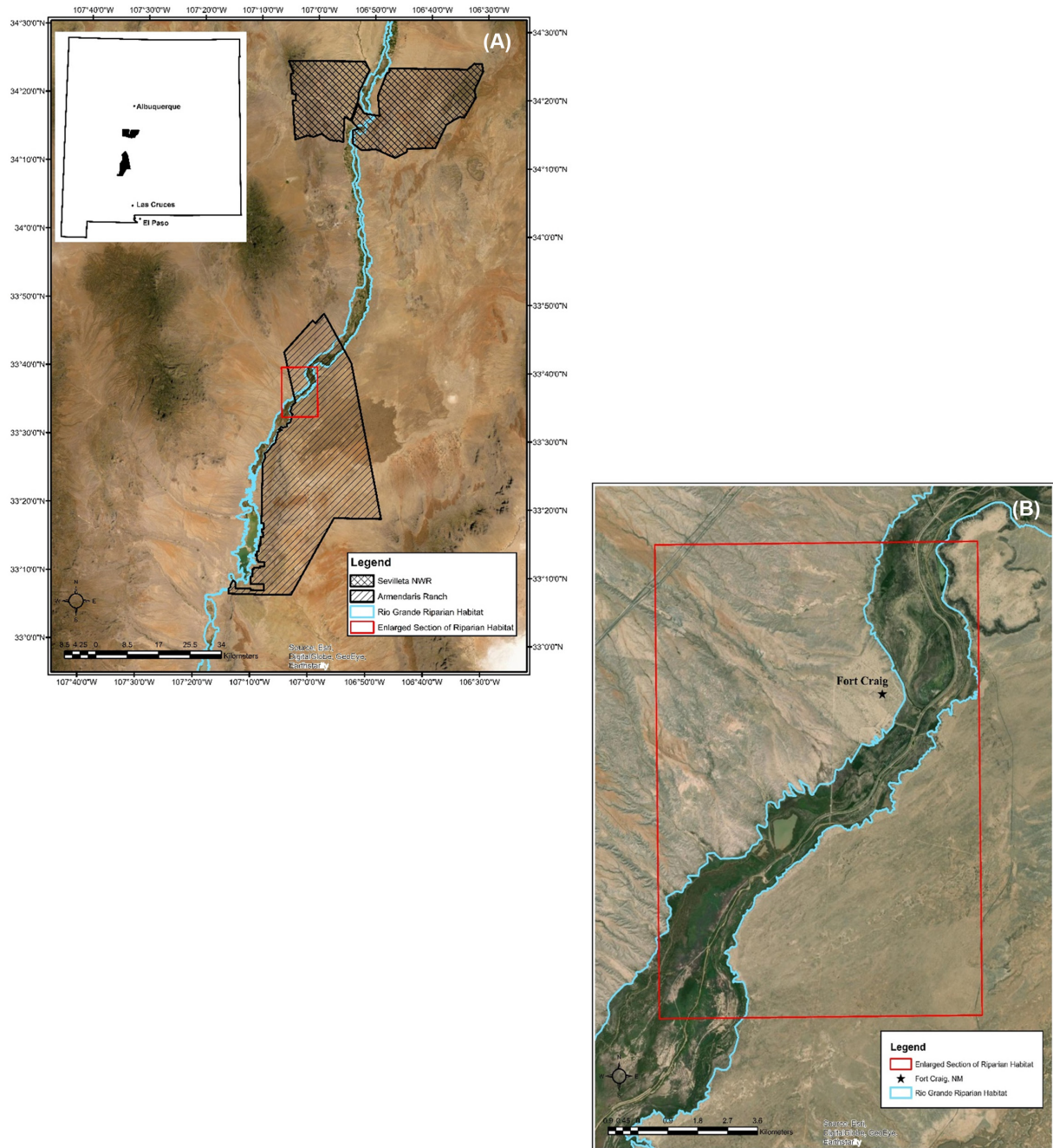


Figure 1. (A) Location of Sevilleta National Wildlife Refuge (north), Armendaris Ranch (south), and Rio Grande riparian bosque habitat (blue) in south-central New Mexico where we collected data on puma kills and prey diversity. Predation data were collected from GPS-collared pumas from 2016 to 2018 at the Sevilleta National Wildlife Refuge and from 2014 to 2018 at the Armendaris Ranch. (B) 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 to 2018.

Los Pinos and Sierra Ladrones 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 Los Pinos and Sierra Ladrones. The vegetation within the Rio Grande bosque is not only nearly identical to the AR but also has some restored wetland and waterfowl management areas. In the uplands, the SNWR has more pinyon pine, oak *Quercus grisea*, *Q. gambelii*, and juniper than the AR. The temperatures range from an average daily minimum of 2.1°C

(SD \pm 4.3) in January to an average daily high of 25.2°C (SD \pm 2.6) in July. Mean annual rainfall is 20.6 cm (SD \pm 6.6), with a mean annual snowfall of 11.8 cm (SD \pm 12.2; climate data from Bernardo, NM, 1936–2019; WRCC 2018b).

Common mammals in the upland desert areas at the SNWR include elk, non-native aoudad *Ammotragus lervia*, Rocky Mountain bighorn sheep, 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 game bird 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.

The abundance, availability and vulnerability of various prey species can change seasonally in our study area. To account for seasonal differences in prey composition, we used long-term climate data (1936–2019) to classify seasons at both study areas as the cool–dry (CD, November–March), hot–dry (HD, April–June), and hot–wet (HW, July–October) seasons.

Capture and monitoring

We 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. We monitored snare sets using cellular cameras (Verizon Blackhawk, Covert Scouting Cameras, Lewisburg, KY) and we used VHF trap-site transmitters (TBT-503-3, Telonics Inc., Mesa AZ) to monitor snares in areas lacking cellular service. We programmed the cellular cameras to send an SMS picture message alert immediately upon activity at the snare and tested the cameras for functionality by sending a remote command to the cameras to send a real-time image of snare sites daily at 07:00 and 18:00 h (MST). When using VHF trap-site transmitters, we checked the VHF signal every 6–12 h, depending on the weather conditions. We checked the snare transmitters more frequently during periods with hot (above 32°C) and cold (below 0°C) ambient temperatures to reduce the risk of stress or mortality from hyperthermia or hypothermia, respectively. We also used hounds to capture pumas in areas that provided suitable hunting conditions for hounds and safe escape structures (trees or boulders) for pumas. We mostly used hounds to recapture pumas to exchange collars with low batteries or those that were malfunctioning. Upon capture, we immobilized pumas with a pneumatic dart gun using 5 mg kg⁻¹ ketamine combined with 0.08 mg kg⁻¹ medetomidine. We used 0.3 mg kg⁻¹ atipamezole as the antagonist for medetomidine (Kreeger et al. 2002). During processing, we recorded the age, sex and weight of each captured animal. We estimated the age using tooth wear and pelage patterns (Shaw 1986). We collared pumas older than 10–12 months with a GPS-Iridium collar (G2110E, Advanced Telemetry Systems, Isanti, MN). We 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 tag. We closely monitored vital rates of 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).

We 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. 19:00 – 07:00 h; Sweanor et al. 2008, Lewis et al. 2015, Soria-Díaz et al. 2016) and then at 3-h intervals during the daytime (i.e. 10:00, 13:00 and 16:00 h) when pumas are less active. We programmed the collars on the SNWR to collect eight GPS fixes per day at 3-h intervals. The GPS data were transmitted via the Iridium satellite system every 12 h (i.e. 06:00, 18:00 h MST).

Prey composition data collection

We used GPS clusters to identify potential prey kill sites and to determine diet composition. At the AR, we 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-h fix interval, we 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. To make efficient use of limited field resources, we used broader temporal and more restricted distance characteristics than some other studies that used GPS cluster analysis to identify predator kill sites. We used AnimalClusters.R (ver. 1.1) developed by Daniel and Kindschuh (2016) and program R (ver. 3.1.2; <www.r-project.org>) to identify GPS clusters. We then investigated clusters in the field as soon as possible to prevent loss of kill evidence caused by scavengers and weathering, which was generally within 7–14 days of the cluster start date. We also prioritized smaller clusters for visitation to minimize the loss of evidence from clusters that might contain remains of smaller prey species. We 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. Thus, we 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). We classified clusters as kill sites if they contained evidence of a kill.

At each kill site, we used tooth wear, pelage patterns and the morphological characteristics of the carcass to estimate the age class of prey. For ungulate prey, we classified ages as neonate (<1 year), yearling (1–2 years), sub-adult (2–4 years), adult (4–6 years), (older than 6 years), and unidentified for prey that lacked evidence of age. For non-ungulate prey, we classified age as neonate (younger than 1 year), adult (older than 1 year), and undefined. We used genitalia or secondary sexual characteristics to identify prey sex when possible. We determined if the prey 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). We also used the rate of decomposition of the carcass relative to the GPS location fix times and dates from the cluster (Wilckens et al. 2015). We inspected the carcass remains for signs of malady, injury, deformity or anything that could have increased its susceptibility to puma predation.

Analyses

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 the predominant use of one vegetation cover type over others by GPS-collared pumas, we used satellite imagery in ArcGIS 10.6 (Esri 2018: 10.6. Redlands, CA) to digitize the boundary between the riparian bosque along the Rio Grande and the xeric uplands (Fig. 1). We 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 GPS 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.

We categorized prey species into four prey classes: avian (all non-waterfowl avian species), aquatic (all species with habitat requirements associated with water in the Rio Grande, including fish, turtles, waterfowl, beaver and muskrat), small mammal (all non-ungulate mammals), and ungulate prey. We combined beaver and muskrat with aquatic species because their populations in our study area would not exist without the aquatic habitat created by the Rio Grande. We did not document any beaver or muskrat kills outside of the riparian habitat and all kills were located at very close proximities to water, identical to the other aquatic species documented (carp, turtles). We then calculated the proportion of kills in each prey class for individual pumas within each season and year. Because our response variables were proportional, we then used the logit transformation on the data before analysis. We 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). We 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, we 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 SPSS Statistics for Windows, ver. 25.0).

Results

We captured 11 pumas (7 male and 4 females) on the AR between February 2014 and June 2018 and 5 pumas (1 male and 4 females) on the SNWR from November 2015 through December 2017 (Table 1). Only one female puma was captured using hounds, the others were captured with snares. Data were 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. Most of the pumas in this study were classified as adults (>3 years) however we did collect data from 3 subadult (18 months to 3 years) pumas at the AR (2 females, 1 male). We classified 3 males and 4 females

Table 1. Puma sex, age, monitoring period, 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, 2014–2018. Puma habitat classification based upon the proportion of fixes within habitat type; riparian bosque or upland desert.

Puma ID	Sex	Age (years)	No. of days monitored (No. GPS fixes)	No. kills	Proportion of GPS fixes in upland/riparian habitat	Puma classification	Proportion of kills per prey class			
							Aquatic (%)	Avian (%)	Small mammal (%)	Ungulate (%)
ARF01	F	4–6	712 (8668)	81	3%/97%	riparian	48	1	23	27
ARF02	F	2	183 (2550)	48	2%/98%	riparian	83	4	8	4
ARF03	F	4–5	326 (4468)	57	100%/0%	upland	0	5	49	46
ARF05	F	1–2	530 (7000)	65	8%/92%	riparian	15	6	63	15
ARM011	M	6	144 (1874)	19	57%/43%	mixed	0	0	16	84
ARM041	M	4	53 (768)	12	56%/44%	mixed	33	0	58	8
ARM051	M	1–2	491 (6554)	74	12%/88%	riparian	28	11	32	28
ARM061	M	5–6	162 (1959)	19	84%/16%	upland	11	0	21	68
ARM07	M	4–6	597 (7606)	83	18%/82%	riparian	39	0	17	45
ARM09	M	8–9	461 (6001)	50	92%/8%	upland	0	0	12	88
ARM101	M	5	54 (1211)	8	53%/47%	mixed	0	0	0	100
LM71	M	4–5	151 (920)	15	96%/4%	upland	0	0	0	100
SEVF01	F	3–4	490 (3866)	19	100%/0%	upland	0	0	5	95
SEVF02	F	3	126 (1072)	12	3%/97%	riparian	67	0	8	25
SEVF03	F	3–4	563 (3800)	58	90%/10%	upland	0	0	43	57
SEVF04	F	5–6	512 (5562)	63	100%/0%	upland	0	0	24	76
SEVM01	M	5	27 (341)	3	51%/49%	mixed	67	0	0	33

¹Pumas were removed for bighorn depredation during this study. Male puma ARM04 was also removed due to public safety concerns.

as being upland pumas, 2 males and 4 females as riparian pumas and 4 males as mixed pumas (Table 1). We monitored the pumas for 5582 telemetry days ($n=17$ pumas, mean = 328 days/puma \pm 226 days [SD]; Table 1). Female pumas were generally monitored for a longer period (3442 total days; mean = 430 days/female \pm 200 days [SD]) than males (2140 days; mean = 237 days/male \pm 217 [SD]). We monitored pumas for 2457 telemetry days during the cool-dry seasons, 1195 telemetry days during the hot-dry seasons, and 1930 telemetry days during the hot-wet seasons.

We investigated 1073 GPS clusters, of which 686 (64%) were kills or feeding sites. The remaining 387 cluster locations we 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%). We found 531 kills on the AR (77%) and 155 kills at SNWR (23%). Female pumas killed 403 prey animals (59% of total kills) and males killed 283 (41% of total kills).

We 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 common 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 18 kills of avian species (0.03%), 158 kills of aquatic species (23%), 192 kills of small mammal species (28%), and 318 ungulate kills (46%; Table 2). We were 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 we were able to collect age information, there were 55 neonates (8%), 46 yearlings (7%), 68 sub-adults (10%), 275 adults (40%), and 28 mature animals (4%). There were 214 kills with insufficient remains to adequately estimate the age of the animal (31%). We were able to identify the sex for 76 male (11%) and 55 female (8%) prey, most of which were adult ungulates ($n=118$; 90%). There were 555 kills (81%) that lacked genitalia or secondary sexual characteristic to determine the

Table 2. Puma kills by species documented at GPS clusters from collared pumas at the Armendaris Ranch and Sevilleta National Wildlife Refuge in south-central New Mexico, 2014–2018.

Prey class	Prey species	No. killed	Percent of total kill sites (%)	No. prey kills per season ¹		
				Cool-dry	Hot-dry	Hot-wet
Avian	American crow <i>Corvus brachyrhynchos</i>	3	<0.5	0	3	0
	Red-tailed hawk <i>Buteo jamaicensis</i>	1	<0.5	1	0	0
	Rio Grande turkey <i>Meleagris gallopavo intermedia</i>	6	1	0	2	4
	Various non-waterfowl species	8	1	6	1	1
Total avian kills		18	3	7	6	5
Aquatic	Beaver <i>Castor canadensis</i>	70	10	34	14	22
	Common carp <i>Cyprinus carpio</i>	49	7	9	22	18
	Channel catfish <i>Ictalurus punctatus</i>	1	<0.5	0	0	1
	Muskrat <i>Ondatra zibethicus</i>	1	<0.5	0	1	0
	Waterfowl	21	3	11	3	7
	Spiny softshell turtle <i>Apalone spinifera</i>	16	2	1	0	15
Total aquatic kills		158	23	55	40	63
Small mammal	Badger <i>Taxidea taxus</i>	7	1	4	0	3
	Bobcat <i>Lynx rufus</i>	5	1	1	3	1
	Desert cottontail <i>Sylvilagus audubonii</i>	3	<0.5	2	0	1
	Coyote <i>Canis latrans</i>	84	12	48	13	23
	Domestic dog	1	<0.5	1	0	0
	Gray fox <i>Urocyon cinereoargenteus</i>	19	3	2	0	17
	Jackrabbit <i>Lepus californicus</i>	5	1	1	1	3
	Kit fox <i>Vulpes macrotis</i>	1	<0.5	1	0	0
	Porcupine <i>Erethizon dorsatum</i>	2	<0.5	1	0	1
	Raccoon <i>Procyon lotor</i>	51	7	35	3	13
	Ring tail <i>Bassariscus astutus</i>	1	<0.5	1	0	0
	Skunk-spotted <i>Spilogale gracilis</i> , striped <i>Mephitis mephitis</i> , hog-nosed <i>Conepatus leuconotus</i>	13	2	8	4	1
	Total small mammal kills		192	28	105	24
Ungulate	Bighorn sheep <i>Ovis Canadensis nelsoni</i>	27	4	19	1	7
	Cattle <i>Bos taurus</i>	5	1	4	1	0
	Elk <i>Cervus canadensis</i>	13	2	3	2	8
	Feral goat <i>Capra hircus Linnaeus</i>	1	<0.5	1	0	0
	Collared peccary <i>Peccary tajacu</i>	21	3	14	2	5
	Mule deer <i>Odocoileus hemionus</i>	195	28	74	11	110
	Gemsbok <i>Oryx gazella</i>	35	5	18	10	7
	Pronghorn <i>Antilocapra americana</i>	21	3	5	4	12
Total ungulate kills		318	46	138	31	149
Total kills		686	100	305	101	280

¹Seasons were defined as cool-dry (Nov–Mar), hot-dry (Apr–Jun) and hot-wet (Jul–Oct).

sex. We documented 305 kills during the cool-dry season (44%), 101 during the hot-dry season (15%) and 280 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%) and hot-wet ($n=22$; 8%). Carp were the most frequent prey species located at GPS clusters 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 four 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. 2). Kill sites from upland pumas were comprised of 2–3 times as many ungulates as riparian and mixed pumas using both areas (Fig. 2). Small mammal prey were more prevalent at the kill sites of upland (21 total, mean proportion = 0.217 ± 0.051 [SE]) and riparian pumas (18 total, mean proportion = 0.249 ± 0.063 [SE]) compared to mixed pumas that used both areas (12 total, mean proportion = 0.064 ± 0.049 [SE]; Fig. 2).

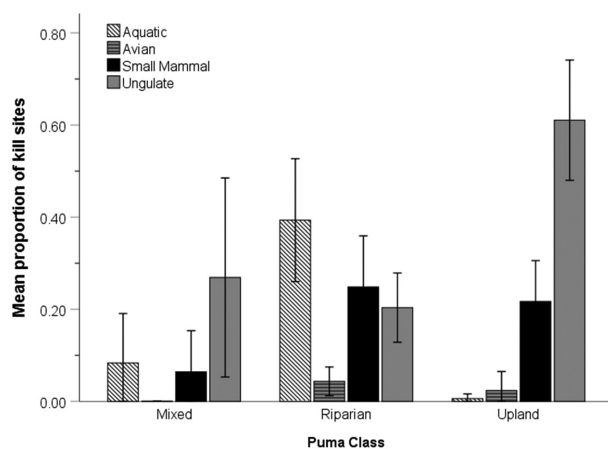


Figure 2. Mean proportion of puma kill sites by prey class and puma habitat class based on GPS-collared pumas in the Armendaris Ranch and Sevilleta National Wildlife Refuge, south-central New Mexico, 2014–2018. Pumas are categorized into habitat classes based on the proportion of their GPS fixes within the upland desert and Rio Grande riparian bosque habitats. Error bars represent 90% confidence intervals.

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 (Fig. 3). The proportion of kills composed of small mammal prey differed by puma habitat classes and puma sex (puma habitat class \times puma sex interaction; $F_{1,52} = 3.32$, $p = 0.077$, Fig. 4). 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. The proportion of kill sites composed of avian prey were dependent on puma habitat class, season, and sex (puma habitat class \times season \times 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 (Table 3).

Ungulate prey comprised the highest mean proportion of kills across all three seasons with the highest during the hot-wet season (0.524 ± 0.091 [SE]). There was more aquatic prey killed during the hot-dry season ($n=40$ aquatic prey, $n=31$ ungulate prey), however, the mean proportion of ungulates (0.235 ± 0.079 [SE]) in the combined diet was still higher than that for aquatic prey (0.189 ± 0.087 [SE]). Small mammal prey had the second highest mean proportion during the cool-dry (0.239 ± 0.057 [SE]) and hot-wet (0.155 ± 0.041 [SE]) seasons but had a slightly lower mean proportion than aquatic prey during the hot-dry season (0.183 ± 0.075 [SE]). Avian prey represented the lowest mean proportion of the diet across all three seasons with the highest proportion during the hot-dry season (0.041 ± 0.031 [SE]) and lowest during the hot-wet season (0.012 ± 0.009 [SE]; Fig. 3).

Discussion

We identified high variability in puma prey composition as a result of different habitat conditions and prey availability between the mesic riparian bosque along the Rio Grande and surrounding Chihuahuan Desert. The diet breadth documented in many previous puma studies is often less than 20 different prey species. Approximately 15 different species were consumed by jaguars and pumas in Sonora, Mexico

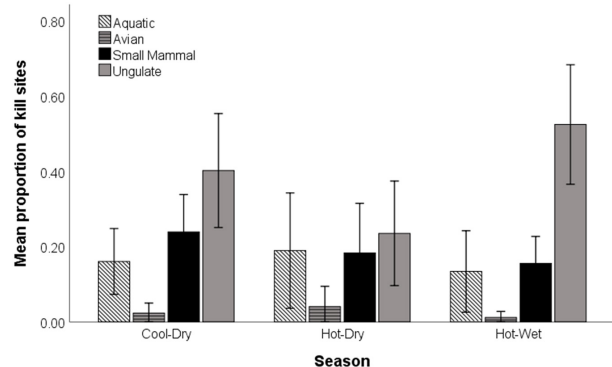


Figure 3. Mean seasonal proportion of puma kill sites by prey classes of GPS-collared puma at the Armendaris Ranch and Sevilleta National Wildlife Refuge in south-central New Mexico, 2014–2018. Error bars represent 90% confidence intervals.

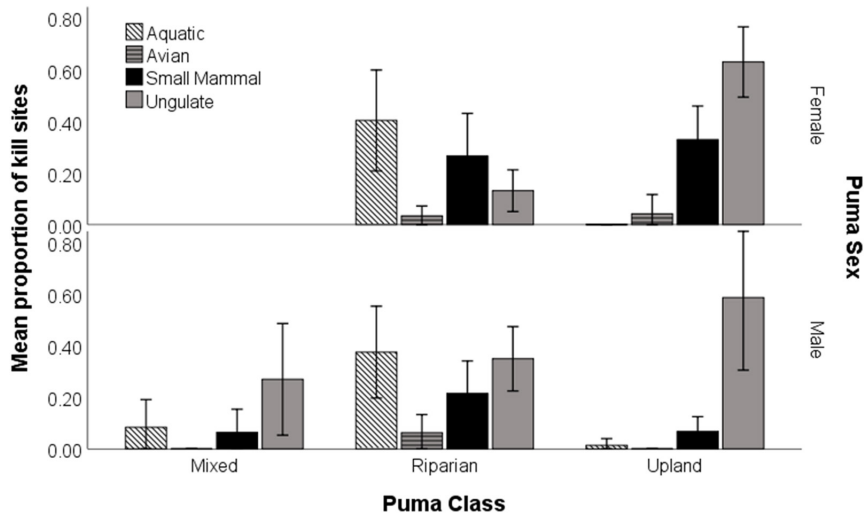


Figure 4. Mean proportion of puma kills by prey class, puma sex, and puma habitat class based on GPS-collared pumas at the Armendaris Ranch and Sevilleta National Wildlife Refuge, south-central New Mexico, 2014–2018. Pumas are categorized into habitat classes based on the proportion of their GPS fixes within the upland desert and Rio Grande riparian bosque habitats. Error bars represent 90% confidence intervals.

(Rosas-Rosas et al. 2003), 17 different species in northeast Oregon (Clark et al. 2014), 13 species in the badlands of North Dakota (Wilckens et al. 2015), 15 species in the Maya Biosphere Reserve, Guatemala (Novack 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 and Quigley (2019) reported pumas consuming more than 40 different species in the Greater Yellowstone Ecosystem, Wyoming. Most previous puma diet studies in desert areas occurred mostly 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.

Although we documented higher diversity in prey composition than in many previous puma studies in desert biomes, our results are still similar in that large ungulate, primarily deer, are the most common prey consumed (Logan and Sweanor 2001, de la Torre and de la Riva 2009, Villepique et al. 2011, Wilckens et al. 2015). The specific prey composition of pumas restricted to the upland areas strongly suggests that had the landscape been homogenous desert without the riparian bosque, our 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). However, Logan and Sweanor (2001) did not use GPS collars during their study, so kills were likely biased towards larger prey items, whereas in our study we identified several kills associated with smaller prey using GPS cluster analyses. The diets of the upland pumas in our study consisted of 70% ungulate prey, 28% small mammal prey, and 2% aquatic and avian prey. Prey composition at kill sites of riparian pumas was similar to those in 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, Gómez-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 was a common prey 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 and 38% small mammal and aquatic prey. Female pumas were spent 90–100% of their time within their chosen habitat and utilized all prey classes. Whereas males utilized both habitats more generally, spending 53–96% of their time within a single habitat type but kill composition was less diverse compared to females.

Elk kills were uncommon and only comprised 2% of the total kills we documented. Elk occurred at lower densities in our 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; Fig. 1) and at higher elevations on the SNWR, which limited their availability as potential prey. Gemsbok, an elk-size non-native ungulate, occurred at higher densities (Bender et al. 2019) and were frequently preyed upon by male pumas (3 males were responsible for 89% of gemsbok kills we documented) and infrequently by female pumas (2 females killed 3 gemsbok). Predation of adult gemsbok was unexpected, as only 3 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 and semi-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 we 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%

Table 3. Puma kills by age and sex documented at GPS clusters from collared pumas at the Armendaris Ranch and Sevilleta National Wildlife Refuge in south-central New Mexico, 2014–2018.

Prey class	Prey species	No. prey kills per prey sex			No. prey kills per prey age class						
		Male	Female	Unidentified	Neonate	Yearling	Sub-adult	Adult	Mature	Unidentified	
Avian	American crow	0	0	3	0	0	0	0	0	0	3
	Red-tailed hawk	0	0	1	0	0	0	1	0	0	0
	Rio Grande turkey	2	0	4	0	0	1	3	0	0	2
	Non-waterfowl	0	0	8	0	0	0	0	0	0	8
Total avian kills	Beaver	2	0	16	0	0	1	4	0	0	13
	Common carp	2	0	68	0	0	2	44	2	0	22
	Channel catfish	0	0	49	0	0	0	5	0	0	44
	Muskkrat	0	0	1	0	0	0	1	0	0	0
	Waterfowl	0	0	21	0	0	0	1	0	0	0
	Spiny softshell turtle	0	0	16	0	0	0	5	0	0	16
	Badger	2	0	156	0	0	2	56	0	0	16
	Bobcat	1	0	6	0	0	0	3	2	2	98
	Desert cottontail	0	0	5	0	0	0	2	0	0	2
	Coyote	2	1	81	0	1	2	57	6	6	3
Total aquatic kills Small mammal	Domestic dog	0	0	1	0	0	0	0	0	0	1
	Gray fox	0	0	19	0	0	1	5	0	0	13
	Jackrabbit	0	0	5	0	0	0	0	0	0	5
	Kit fox	0	0	1	0	0	0	1	0	0	0
	Porcupine	0	0	2	0	0	0	2	0	0	0
	Raccoon	3	1	47	0	1	8	21	0	0	21
	Ring tail	0	0	1	0	0	0	0	0	0	1
	Skunk	1	0	12	0	0	0	2	0	0	11
	Bighorn sheep	7	2	183	0	2	11	93	8	8	78
	Cattle	12	5	10	7	1	4	8	6	6	1
	Elk	0	0	5	4	0	1	0	0	0	0
	Feral goat	3	6	4	0	2	5	6	0	0	0
	Collared peccary	0	0	1	0	0	0	1	0	0	0
	Mule deer	38	40	117	37	36	24	68	11	19	19
	Gemsbok	3	0	32	7	5	13	3	0	0	7
Pronghorn	9	2	10	0	0	3	13	0	0	5	
Total ungulate kills Total kills		65	53	200	55	44	53	116	17	33	33
		76	55	555	55	46	67	269	27	222	222

($n=27$) of the ungulate kills. However, the low contribution of bighorn sheep to the prey composition was almost certainly influenced by an active management program that included the lethal removal of pumas that killed multiple (5) bighorn sheep in the Fra Cristobal and Ladron 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, we only documented a few instances of livestock predation and most were beef calves and a feral goat killed in the bosque along the Rio Grande.

The increased proportion of ungulate prey during the hot-wet season is coincident with the increased availability of mule deer fawns during fawning season (July–September). Fawns and yearlings comprised 55% ($n=60$) of the mule deer kills and 21% of the total kills during the hot-wet season. These findings are consistent with Logan and Sweanor (2001) on WSMR and with the findings of Kay (2018) in the nearby Gallinas Mountains near Corona, New Mexico. During the hot-dry season, we documented an increase in aquatic prey consumption; this time coincides with the spawning season of carp. During spawning, carp are more susceptible to puma predation as they use shallower waters (1–4 feet in depth) to spawn. We speculate that carp were typically caught in shallower water of the Rio Grande 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 catch them. One young female puma (ARF02) seemed to specialize (Elbroch and Wittmer 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 (Stebbins 2003), which 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.

Like most studies of predator diet composition using GPS cluster analysis, we were faced with tradeoffs, both between GPS fix interval and collar battery life and when selecting a cluster definition (i.e. number of points, timing and distance) that would improve detection of kill sites from small and large prey species. The longer temporal component of our cluster definition and prioritizing clusters initiated during nocturnal or crepuscular periods likely enhanced our ability to detect larger prey items (Wilckens et al. 2015, Vogt et al. 2018). However, our cluster definition may have also biased against detection of some smaller prey species. The shortened nighttime GPS fix interval and promptness in field investigation

of smaller clusters likely improved our ability to locate some of the smaller prey species (Knopff et al. 2009). Nonetheless, we 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 our data (Bacon et al. 2011). For the rabbit kills that we were able to locate, typically only feet, ears (jackrabbit), or a few tufts of fur remained as evidence similar to other studies (Elbroch and Wittmer 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). We were unable to investigate some of the clusters that occurred on private lands outside of our study areas and WSMR as promptly due to access restrictions. The delay may have reduced our ability to detect smaller non-ungulate prey at those sites.

Previous research on pumas across ecosystems ranging from northern Canada to the southern tip of South America indicates that puma are generalist predators and frequently kill the most abundant and or vulnerable prey species in the areas they occupy. The heterogeneity across a relatively small spatial scale in our unique study system, increased prey diversity for pumas. Pumas show similar adaptive responses across much larger spatial scales. The diverse diets of the pumas in our study provide 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 ranges encompass. Additionally, puma diet is likely to be more diverse in areas with heterogeneous habitat conditions that support a wider variety of prey species. This is especially true in western North America where xeric habitat conditions typically do not support higher densities of ungulate prey and pumas are forced to exploit a variety of smaller species.

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Permits – 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).

Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.pk0p2ngpb>> (Prude and Cain III 2021).

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