ASSESSING HABITAT RELATIONSHIPS OF MOUNTAIN LIONS AND THEIR PREY IN THE DAVIS MOUNTAINS, TEXAS

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ABSTRACT—Availability and habitat use are central factors in the selection of prey by mountain lions (*Puma concolor*), and they are important for understanding predator–prey dynamics. We used an array of camera traps to evaluate the relative abundance and spatial distribution of mountain lions and their prey in the Davis Mountains of Texas. Resource selection was evaluated for four criteria: elevation, ecological system, fine-scale terrain ruggedness, and broad-scale terrain ruggedness. We used χ^2 analysis to determine whether habitat was used in proportion to availability, and then we calculated a selection index with 95% confidence intervals using a Bonferroni adjustment. We found feral hog (*Sus scrofa*) to be the most abundant species, composing 23% of the total animals observed. Feral hog and gray fox (*Urocyon cinereoargenteus*) were the most widespread species, each observed at 33 of 38 camera locations. For each prey species evaluated, habitat use differed significantly from availability for at least one of the four resource criteria. Mountain lion use of resource criteria was not different from availability, except they avoided the second lowest class of broad-scale terrain ruggedness. With knowledge of mountain lion habitat use and the availability of prey, resource managers can better assess what effects mountain lion predation may have on a specific species, thereby allowing for better management of those species.

RESUMEN—La disponibilidad y uso de hábitat son factores principales al escoger las presas para los pumas (*Puma concolor*) y además son factores importantes para entender la dinámica entre el depredador y su presa. Distribuimos trampas cámaras para evaluar la abundancia relativa y distribución espacial de pumas y su presa en las Davis Mountains en Texas. La selección de recursos se evaluó en 4 categorías: elevación, sistema ecológico, irregularidad de terreno a pequeña escala, e irregularidad de terreno a gran escala. Utilizamos el análisis χ^2 para determinar si el hábitat fue utilizado en proporción a la disponibilidad y después calculamos el índice de selección con intervalos de confianza de 95% utilizando un ajuste de Bonferroni. Encontramos al cerdo silvestre (*Sus scrofa*) como la especie más abundante, correspondiendo al 23% del total de animales observados. El cerdo silvestre y la zorra gris (*Urocyon cinereoargenteus*) fueron las especies con mayor distribución, cada una observada en 33 de los 38 lugares con cámaras. Para cada especie evaluada, el uso de hábitat fue significativamente diferente de la disponibilidad para al menos uno de las cuatro categorías de recursos. El uso de recursos por pumas no fue diferente al disponible excepto que evitaron la segunda clase más baja de irregularidad de terreno a gran escala. Con la información de uso de hábitat por el puma y la disponibilidad de presas, los administradores de recursos naturales pueden evaluar mejor los efectos de la depredación por el puma en especies específicas, lo cual permitirá un mejor manejo de esas especies.

Prey availability and distribution are important factors in the survival and land use of any predator species. Knowledge of the availability of prey in an area can be used to predict predator abundance and habitat use (Khorozyan et al., 2008). Optimal foraging theory suggests that predators will select for the most energetically profitable prey (Emlen, 1966). This is demonstrated by a gradient in the average size of mountain lion (*Puma concolor*) prey based on latitude. In areas closest to the equator, mountain lions prey generally on animals <15 kg, whereas in the far northern and southern reaches of their range, mountain lions mainly prey on large ungulates such as deer (*Odocoileus*) and elk (*Cervus elaphus*) (Logan and Sweanor, 2001).

Studies in the United States, particularly in Texas, have consistently shown deer to be the main prey of North American mountain lions (Iriarte et al., 1990; McKinney, 1996). There is some evidence that mountain lions will select for deer in greater abundance than they are available on the landscape (Harveson et al., 2000; Villepique et al., 2011), but evidence also shows they will shift toward preying upon other species when there is a decrease in the deer population (Leopold and Krausman, 1986). Determining the relative abundance and distribution of prey is an important initial step in understanding the predatory behavior of mountain lions in an area and for assessing its potential impact on prey species.

One way to better understand the spatial distribution of any species is to study its resource selection habits; selection indices provide a simple and intuitive approach to doing so. Resource managers can use information on habitat preference and avoidance to predict where a species is most likely to be found (Manly et al., 2002). Habitat preferences can also factor into local and regional carrying capacity (Bowkett et al., 2007). By evaluating the habitat selection of both predators and prey, we can gain insight into the interaction of these species. Selection of habitat by herbivore and mesopredator species generally reflects a balance between protection from predators and access to foraging resources (Pierce et al., 2004; Kelly and Holub, 2008). Meanwhile, mountain lions, as apex predators, are expected to select for areas that will provide adequate prey while also providing the cover necessary for hunting (Dickson and Beier, 2002). By knowing what habitat the mountain lion population prefers in an area, and by comparing this preference to the habitat use of their expected prey, better predictions can be made regarding which species mountain lions might be expected to prey upon most heavily.

In recent years, camera traps have become an important tool in wildlife research and management. Although camera traps have most often been used for surveying carnivore species (Foster and Harmsen, 2012), they also have proven useful in surveying a wider range of species, including birds, small mammals, and ungulates (Watts et al., 2008; Bengsen et al., 2011; O'Connell et al., 2011). Camera traps provide a tool to more thoroughly survey species over a large area than may be possible with other survey techniques, particularly in remote areas with rough terrain (Silveira et al., 2003).

We used an array of camera traps to observe mountain lions and their prey in the Davis Mountains of western Texas. Our objectives were to 1) describe the overall species makeup, including relative abundance and distribution of species; 2) assess mountain lion use of resources within the study site; and 3) describe the distribution of the principal mountain lion prey species in the Davis Mountains as it relates to resource availability and to the probability of presence of mountain lions.

Materials and Methods—*Study Area*—The Davis Mountains are located in the Chihuahuan Desert of far western Texas and form a sky island within the Sierra Madre Oriental sky island complex. The Davis Mountains range consists mainly of rugged igneous mountains, remnant of a volcanic field, with broad valleys and steep canyons cut by intermittent streams (Blair, 1940). The total mountain range covers an area of roughly 5,200 km^2 (Anderson, 1968). Average annual precipitation is 50.98 cm (National Climatic Data Center, http://www.ncdc.noaa.gov/cdo-web/datatools/normals). A variety of habitats, cooler temperatures, and relatively abundant water make the Davis Mountains a haven for a diverse array of species (DeBano et al., 1995).

The study site is located on 34,200 ha at the heart of the Davis Mountains on The Nature Conservancy's Davis Mountain Preserve and two adjacent private ranches. Elevations within the study site range from 1,368 to 2,554 m at the top of Mount Livermore. Within the study site, the major vegetation types found on the mountain slopes and rolling landscapes include Mexican pinyon pine (*Pinus cembroides*) and juniper (*Juniperus*) shrublands and woodlands, gray oak (*Quercus grisea*) savannas and woodlands, and ponderosa pine (*Pinus ponderosa*) and oak (*Quercus*) woodlands and forests interspersed with mountain grasslands. In the canyons and along streams and drainages, major vegetation types include shrublands consisting of species such as seepwillow (*Baccharis salicifolia*), catclaw mimosa (*Mimosa aculeatacarpa* var. *biuncifera*), and Apache plume (*Fallugia paradoxa*), as well as forests and woodlands dominated in some areas by pine (*Pinus*) and juniper species, and in other areas by deciduous hardwoods such as chinkapin oak (*Quercus muehlenbergii*) and bigtooth maple (*Acer grandidentatum*) (Elliot et al., in litt.).

Field Methods—We placed paired trail cameras at 38 locations throughout the study area. To determine camera locations, a grid was overlaid on the study area, with each grid square encompassing 9 km^2. We placed one camera pair in each grid square. Camera locations were placed an average of 2–3 km apart to allow for adequate coverage of a large study area (Kelly et al., 2008). Cameras were placed strategically in areas determined most likely to capture pictures of mountain lions and their prey. On a large scale, we identified likely travel corridors such as canyon intersections and saddles of mountains. Within these travel corridors, we placed cameras along game trails or dirt roads to maximize the likelihood of capturing wildlife passing through the area. Two cameras facing one another were placed at each location to increase the likelihood of capturing and identifying animals. Pairing of cameras also provided a backup in the case of camera malfunction.

We used a variety of trail camera models, including Bushnell TrophyCam (Bushnell Corporation, Overland Park, Kansas); Moultrie I40, I60, and I90 models (Moultrie Feeders, Alabaster, Alabama); Stealth Cam STC-I850 and Rogue IR models (GSM Outdoors, Grand Prairie, Texas); and Wildview Infrared Extreme (GSM Outdoors, Grand Prairie, Texas). Cameras were activated at each site for a minimum of 3 months between June 2012 and March 2013. Each camera was set to record the date and time of all photos taken. Cameras were set to a three-picture burst to increase the likelihood of capturing an identifiable image, and had a 5-min delay after each burst of pictures to extend battery life and decrease likelihood of multiple detections of the same animal.

We checked cameras every 1–6 months, depending on the remoteness of the camera site. During camera checks, secure digital memory cards were replaced, batteries were checked and changed as needed, and any malfunctioning cameras were replaced.

Photo Analysis—All photos were renamed with the date and time using the open-source program ReNamer (ReNamer version 5.60; www.snapfiles.com/get/denrenamer). Any incorrect dates or times were corrected based on data from the other camera at the site. Photos were sorted by species and number of individuals according to the methods of Harris et al. (2010).

Photos with no visible animal, or with an unidentifiable animal present, were sorted as "unknown." Analysis was performed using the open-source programs DataOrganize (DataOrganize version 1.2, www.smallcats.org/files/DataOrganize.exe) and DataAnalyze (DataAnalyze version 1.8, www.smallcats.org/files/DataAnalyze.exe). Any detections of the same species of animal at the same site within 1 h of each other were considered to be photos of the same individual(s) and thus were not considered independent detections.

Resource Selection—For the main prey species observed, as well as mountain lions, we evaluated four criteria of resource selection: ecological system, elevation, fine-scale terrain ruggedness, and broad-scale terrain ruggedness. We used ArcGIS version 10.0 (ESRI, Redlands, California) to determine the appropriate category at each camera location for each of the four criteria.

We assigned each camera location to one of seven ecological systems based on the Ecological Systems Classification of Texas (Elliot et al., in litt.). The Madrean Encinal (Encinal) ecological system contained four camera locations, the Madrean Lower Montane Pine-Oak Forest and Woodland (Pine-Oak) ecological system contained four locations, and the Madrean Mesic and Canyon Forest and Woodland (Mesic and Canyon) ecological system contained 14 locations. The Madrean Pinyon-Juniper Woodland (Pinyon-Juniper) ecological system contained six locations and the North American Warm Desert Lower Montane Riparian Woodland (Lower Montane Riparian) ecological system contained eight locations. Two ecological systems, the Madrean Oriental Chaparral and the North American Warm Desert Riparian Woodland and Shrubland, each contained only one location and were excluded from analysis due to low sample size.

Elevations at camera locations ranged from 1,468 to 2,460 m. Locations were grouped into three elevation classes: low (<1,700 m, $n = 12$ locations), mid (1,700–1,900 m, $n = 13$ locations), and high (>1,900 m, $n = 13$ locations).

To find the terrain ruggedness level for each location, we used ArcGIS version 10.0 (ERSI) to create a vector ruggedness measure (VRM) using a 5×5 neighborhood from a 30-m digital elevation model map. VRM values range from 0 to 1, with 1 being the most rugged (Sappington et al., 2007). The values from the original VRM map were used as the fine-scale VRM values, as they only take into account the ruggedness directly around the camera site, over an area of 0.0225 km^2. To calculate broad-scale VRM values, we aggregated the original VRM map, which calculated the mean VRM value over a 1.1025-km^2 area.

Fine-scale VRM values within the study site ranged from 0.000003 to 0.265615, and these values were grouped into six equal area VRM classes. Class 1 included VRM values $\leq$0.001044; however, no camera locations were located in this class, so selection for this class was not analyzed. Class 2 ranged from >0.001044 to $\leq$0.004169 and contained three locations. Class 3 ranged from >0.004169 to $\leq$0.008335 and contained four locations. Class 4 ranged from >0.008335 to $\leq$0.014585 and contained six locations, and class 5 ranged from >0.014585 to $\leq$0.027085 and contained seven locations. The remaining 18 locations were in class 6, with all values >0.027085.

Broad-scale VRM values within the study site ranged from 0.000037 to 0.045107, and these values were grouped into five equal area classes. Class 1 included VRM values $\leq$0.004986 and contained three locations. Class 2 ranged from >0.004986 to $\leq$0.009758 and contained six locations. Class 3 ranged from >0.009758 to $\leq$0.014000 and contained nine locations, and class 4 ranged from >0.014000 to $\leq$0.018595 and contained 10 locations. The remaining 10 locations were in the most rugged, class 5, with all values >0.018595.

For each species at each of the four criteria, we performed a χ^2 analysis to determine whether habitat use was in proportion to availability. We then calculated the selection index $w_i = o_i/p_i$, where o_i represents use of the resource and p_i represents availability of the resource, with 95% confidence intervals calculated using a Bonferroni adjustment (Manly et al., 2002). For each species, we determined the number of individual detections within each class of the four criteria, and we used the number of trap days for each class and the total number of detections of that species to calculate the expected detection rate, if all classes had been selected for evenly.

A selection index value >1 indicates selection and a selection index value <1 indicates avoidance. However, to avoid error due to low sample sizes, we only considered a species to be exhibiting avoidance or selection if the 95% confidence interval was entirely below 1, or above 1, respectively (Manly et al., 2002).

RESULTS—*All Species*—We analyzed 250,007 photos in total; 16,156 of these photos had identifiable animals and 3,167 were considered independent. When considering that some pictures contained more than one individual, the total number of independent detections of animals increased to 3,883. All species observed were documented within the first 213 days of the start of the survey. Cameras were deployed for an average of 206 trap days (range = 121–268). Total trap days across the study area was 7,846.

Location H9 (Table 1) was the only camera location where supplemental food and water were available. Over 25% of the photos with identifiable animals came from location H9, including 70% of the detections of javelina (*Pecari tajacu*) and 50% of the detections of deer (*Odocoileus virginianus* and *Odocoileus hemionus*). This site was omitted from the calculation of measures of overall abundance and habitat selection because photo detection rates at this site could not be considered equal to the other sites, which is a requirement for accurate measurement (Jenks et al., 2011). After the removal of site H9, the total number of independent detections was 2,728 and the total trap days across the study area was 7,620. We did include site H9 in the analysis of individual locations and species distributions across the landscape that did not rely on totaling or averaging the number of detections across sites.

No species was observed at all 38 camera locations. Feral hog (*Sus scrofa*) and gray fox (*Urocyon cinereoargenteus*) were the most widespread species, both observed at 33 of 38 locations. Species richness (number of species observed) was 27 across the study area and ranged from 4 to 15 species at individual camera sites. Animals with the most restricted occurrences were vultures (*Cathartes aura* and *Coragyps atratus*); red-tailed hawks (*Buteo jamaicensis*); and a lizard of the family Phrynosomatidae (species unidentifiable), each observed at one site.

Table 1—Most abundant main prey species, number of mountain lion (*Puma concolor*) detections, and fine- and broad-scale terrain ruggedness for all camera locations in the Davis Mountains, Texas, from June 2012 through March 2013. Cameras are sorted by ecological system then by elevation. Prey abundant at individual cameras includes hog (*Sus scrofa*), deer (*Odocoileus virginianus* and *Odocoileus hemionus*), elk (*Cervus elaphus*), coyote (*Canis lantrans*), javelina (*Pecari tajacu*), cow (*Bos taurus*), bobcat (*Lynx rufus*), and aoudad (*Ammotragus lervia*).

Location	Ecological system[a]	Elevation (m)	VRM class (FS, BS)[b]	Most abundant prey	Second most abundant prey	Mountain lion detections
D9	Encinal	1,685	6, 4	Hog	Deer, javelina	0
S4	Encinal	1,718	5, 2	Deer	Javelina	0
H14	Encinal	1,986	3, 4	Deer	Elk	0
D18	Encinal	2,019	4, 3	Elk	Coyote	1
H7	Montane Riparian	1,611	6, 2	Hog	Elk	0
H3	Montane Riparian	1,623	6, 5	Hog	Elk	0
H4	Montane Riparian	1,637	6, 5	Javelina	NA[c]	2
H2	Montane Riparian	1,659	6, 3	Coyote	Hog	3
H5	Montane Riparian	1,692	4, 2	Javelina	Hog	0
H11	Montane Riparian	1,714	5, 3	Hog	Elk	2
H10	Montane Riparian	1,783	4, 1	Coyote	Deer	0
H13	Montane Riparian	1,783	3, 1	Cow	Hog	0
D1	Mesic and Canyon	1,468	6, 5	Hog	Deer, javelina	1
D5	Mesic and Canyon	1,612	6, 5	Hog	Elk	2
D7	Mesic and Canyon	1,612	2, 3	Hog	Elk	2
D4	Mesic and Canyon	1,614	6, 5	Hog	Deer	1
S1	Mesic and Canyon	1,722	6, 4	Hog	Javelina	1
H6	Mesic and Canyon	1,727	5, 3	Javelina	Hog	0
S2	Mesic and Canyon	1,750	6, 4	Javelina	Hog	8
D13	Mesic and Canyon	1,837	6, 3	Hog	Elk	0
D17	Mesic and Canyon	1,850	2, 1	Hog	Coyote	0
D12	Mesic and Canyon	1,907	6, 2	Hog	Coyote	1
D24	Mesic and Canyon	1,924	4, 5	Javelina	Deer	5
D16	Mesic and Canyon	1,941	5, 4	Coyote	Hog	1
D20	Mesic and Canyon	2,056	5, 3	Javelina	Deer	2
D19	Mesic and Canyon	2,145	6, 5	Javelina	Elk	0
H1	Pine-Oak	1,711	6, 3	Hog	Coyote, javelina	0
H9	Pine-Oak	1,902	4, 2	Javelina	Deer	0
D22	Pine-Oak	2,169	3, 4	Hog	Elk	3
D25	Pine-Oak	2,188	6, 4	Deer	Elk, javelina	0
S3	Pinyon-Juniper	1,696	6, 4	Coyote	Javelina	3
H8	Pinyon-Juniper	1,804	3, 5	Elk	Deer	5
H12	Pinyon-Juniper	1,892	4, 3	Deer	Coyote	1
D15	Pinyon-Juniper	1,898	5, 4	Hog	Elk	3
D11	Pinyon-Juniper	1,913	2, 2	Elk	Deer	0
D21	Pinyon-Juniper	1,930	6, 4	Hog	Deer	3
D23	Chaparral	2,461	6, 5	Bobcat	Aoudad	0
D3	Riparian	1,547	5, 5	Javelina	Hog	3

[a] Encinal = Madrean Encinal; Montane Riparian = North American Warm Desert Lower Montane Riparian Woodland; Mesic and Canyon = Madrean Mesic and Canyon Forest and Woodland; Pine-Oak = Madrean Lower Montane Pine-Oak Forest and Woodland; Pinyon-Juniper = Madrean Pinyon-Juniper Woodland; Chaparral = Madrean Oriental Chaparral; Riparian = North American Warm Desert Riparian Woodland and Shrubland.

[b] Terrain ruggedness level was obtained through vector ruggedness measure and then divided into equal area classes across the study area. FS = fine scale; BS = broad scale.

[c] NA = not available.

We did not interpret the number of detections for each species as a measure of absolute abundance because the same individual may be detected on camera multiple times. However, the number of detections for each species was used to estimate the relative abundances of multiple species in comparison to one another (Fig. 1). Ungulates made up more than half of the animals observed, and feral hogs (detections = 618) were the most abundant species across the study site. Coyotes (*Canis latrans*; detections = 275) were the most abundant predator, followed by gray foxes (detections = 205), and at smaller numbers, mountain lions (detections = 54) and bobcats (*Lynx rufus*; detections = 23). The ungulate species observed in the smallest numbers was aoudad

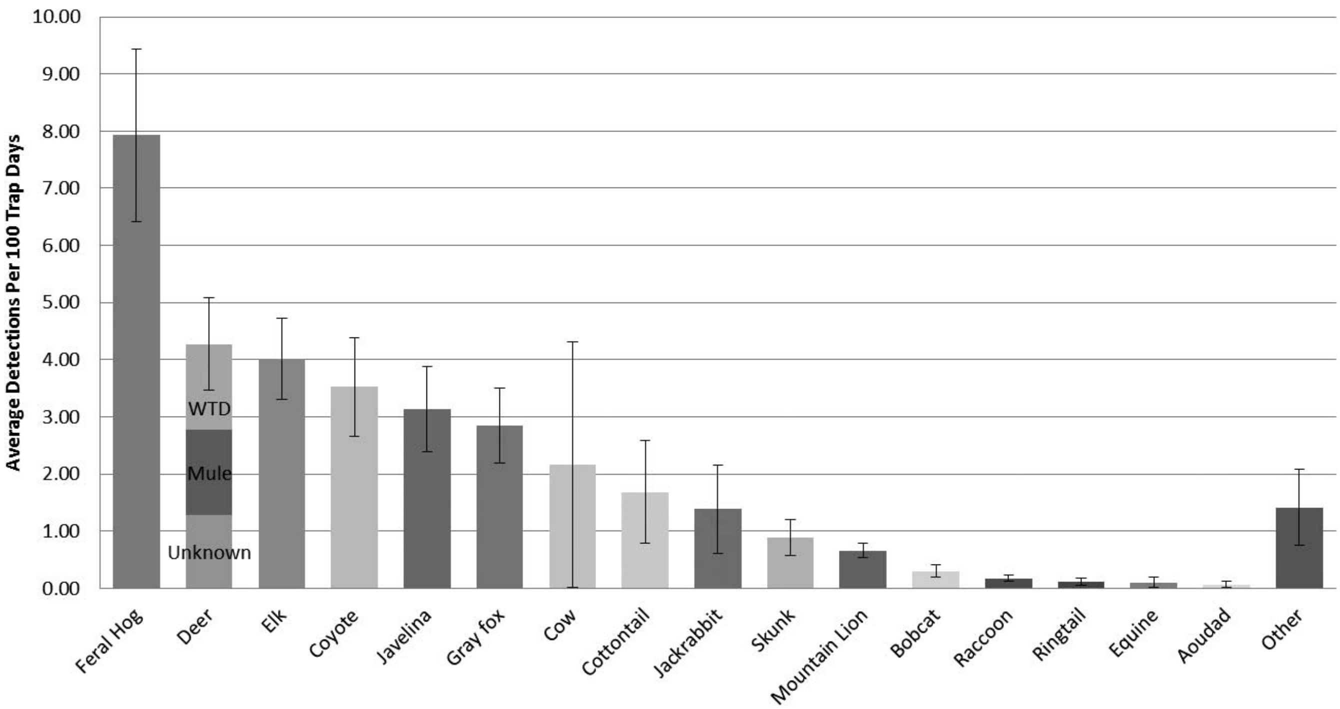

FIG. 1—Relative species abundance, reported as the average detections per 100 trap days with *SE*, for camera sites in the Davis Mountains, Texas, from June 2012 through March 2013. Deer are subdivided as white-tailed deer (WTD), mule deer (Mule), and deer for which we were not able to determine the species (Unknown).

(*Ammotragus lervia*; detections = 6). Other wild species observed at low numbers included ringtail (*Bassariscus astutus*; detections = 7), turkey (*Meleagris gallopavo*; detections = 15), great horned owl (*Bubo virginianus*; detections = 4), and red-tailed hawk (detections = 1). Dogs and humans were left out of the measure of relative abundance as the large majority of detections were of researchers working with this project, and all dogs detected were accompanying humans. Relative abundance varied between ecological systems, as did the overall number of detections per trap day, with detections being highest in the Lower Montane Riparian ecological system and lowest in the Mesic and Canyon and the Encinal ecological systems.

Mountain Lions—Mountain lions were observed at 22 of the 38 camera locations, at a detection rate of 0.71 detections per 100 camera nights (Table 2). Mountain lion use of elevation ranges ($\chi^2 = 0.002$, $df = 2$, $P = 0.9991$), ecological systems ($\chi^2 = 9.354$, $df = 4$, $P = 0.0528$), and fine-scale terrain ruggedness classes ($\chi^2 = 1.622$, $df = 4$, $P = 0.8047$) did not differ significantly from availability. However, mountain lion use of broad-scale terrain ruggedness categories differed significantly from availability ($\chi^2 = 15.635$, $df = 2$, $P = 0.0036$), and the selection index indicted they avoided the second lowest class of terrain ruggedness (Fig. 2).

Major Prey—In describing the major prey species for mountain lions, we considered only those species with an average weight >6.1 kg and therefore likely to be a potential major prey item for mountain lions in this area (Monroy-Vilchis et al., 2009). The species and groups of species observed in this category were feral hog; deer; elk; aoudad; coyote; bobcat; cattle (*Bos taurus*); and horses and mules, with the latter two prey animals being grouped together as equines (*Equus* spp.). The proportion of each major prey species varied between sites and habitat selection varied between species. The overall ratio of mountain lions to their major prey was 1:36.70.

Deer—In approximately 30% of the deer pictures obtained, we were unable to distinguish between white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). Thus, for purposes of this evaluation, we combined white-tailed deer, mule deer, and unidentified deer into the overall "deer" category. In total, 321 individual detections of deer were noted for a total across the study site of 4.21 detections per 100 trap nights. Of those detections, 115 were identified as mule deer (1.51 per 100 trap nights), 109 were identified as white-tailed deer (1.43 per 100 trap nights), and 97 could not be identified to species.

When grouped, deer were the most widespread prey and were observed at 34 of 38 camera locations. Mule deer were positively identified at 26 locations and white-tailed deer at 22 locations. Deer co-occurred with mountain lions at 20 locations. Both white-tailed deer and mule deer separately co-occurred with mountain lions at 13 sites; however, those sites at which they co-occurred were not the same for the two species.

TABLE 2—Summary of photo detections and co-occurrences of mountain lions and their prey in the Davis Mountains, Texas, from June 2012 through March 2013. Data for each species include the total number of independent detections, total and average detections per 100 trap nights, total number of camera locations detected, and the number of locations at which each prey species co-occurred with mountain lions. Scientific names of species are as given in Table 1.

Species	Total independent detections	Total detections per 100 trap nights	Average detections ± *SE* per 100 trap nights	No. of locations detected	No. of locations co-occurred with mountain lions
Mountain lion	54	0.71	0.66 ± 0.13	22	—
All deer	321	4.21	4.28 ± 0.81	34	20
Mule deer	115	1.51	1.49 ± 0.37	26	13
White-tailed deer	109	1.43	1.51 ± 0.37	22	13
Feral hog	618	8.11	7.93 ± 1.51	33	21
Elk	303	3.98	4.01 ± 0.71	31	17
Javelina	244	3.2	3.13 ± 0.75	30	16
Bobcat	23	0.3	0.30 ± 0.10	10	6
Coyote	275	3.61	3.53 ± 0.86	27	15
Aoudad	6	0.08	0.07 ± 0.06	2	1

Both mule deer ($\chi^2 = 21.725$, $df = 2$, $P < 0.0001$) and white-tailed deer ($\chi^2 = 31.583$, $df = 2$, $P < 0.0001$) use of elevation ranges was significantly different than availability, and both avoided the lowest elevation range and selected the mid-elevation range. Use of ecological systems also differed significantly from availability for both mule deer ($\chi^2 = 44.660$, $df = 4$, $P < 0.0001$) and white-tailed deer ($\chi^2 = 11.809$, $df = 4$, $P = 0.0188$). Both mule deer and white-tailed deer selected for the Pinyon-Juniper ecological system and avoided the Mesic and Canyon system. Mule deer was also the only species that selected for the Encinal ecological system. On a fine scale of terrain ruggedness, use by both species of deer differed significantly from availability (mule deer: $\chi^2 = 57.858$, $df = 4$, $P < 0.0001$; white-tailed deer: $\chi^2 = 109.101$, $df = 4$, $P < 0.0001$). Both mule deer and white-tailed deer avoided class 6 and selected for class 4. White-tailed deer also selected for class 2, whereas mule deer avoided it and selected for class 3. Use by mule deer ($\chi^2 = 23.301$, $df = 4$, $P = 0.0001$) and white-tailed deer ($\chi^2 = 122.63$, $df = 4$, $P < 0.0001$) of broad-scale terrain ruggedness classes also was significantly different from availability. White-tailed deer selected for the least rugged terrain, class 1, and avoided the most rugged terrain, classes 4 and 5, whereas mule deer selected for class 3, but also avoided the most rugged terrain, class 5.

Feral Hogs—Feral hogs were the most abundant species, with 8.11 detections per 100 trap nights in total. Feral hogs were observed at 33 of 38 camera locations. They were the prey that most frequently co-occurred with mountain lions, being found together at 21 locations. Within the study site, feral hog use of elevation ranges differed from availability ($\chi^2 = 11.616$, $df = 2$, $P = 0.0030$), as they avoided the highest elevations (e.g., $\geq$1,900 m). Hog use of ecological systems also differed significantly from availability ($\chi^2 = 181.959$, $df = 4$, $P < 0.0001$). They were the only species that selected for the Pine-Oak ecological system. They also selected for the Lower Montane Riparian ecological system, and they avoided all others. On both the fine scale ($\chi^2 = 65.882$, $df = 2$, $P < 0.0001$) and broad scale ($\chi^2 = 91.487$, $df = 2$, $P < 0.0001$), hog use of terrain ruggedness classes was different than availability. On both scales, hogs preferred lower classes of terrain ruggedness, selecting for fine-scale class 3 and broad-scale classes 1 and 2, and avoiding class 4 on the fine scale and class 5 on the broad scale.

Elk—Total detections of elk was 303, for 3.98 detections per 100 trap nights in total. Elk were observed at 31 of the 38 locations, and of those locations, they co-occurred with mountain lions at 17. Elk use differed significantly from availability for elevation ($\chi^2 = 27.122$, $df = 2$, $P < 0.0001$), ecological system ($\chi^2 = 79.099$, $df = 4$, $P < 0.0001$), fine-scale terrain ruggedness ($\chi^2 = 85.711$, $df = 4$, $P < 0.0001$), and broad-scale terrain ruggedness ($\chi^2 = 90.672$, $df = 2$, $P < 0.0001$). Elk selected for the mid-elevation range, whereas they avoided the lowest elevations. They avoided the Mesic and Canyon ecological system and selected for the Pinyon-Juniper and the Lower Montane Riparian ecological systems. On the fine scale of terrain ruggedness, they selected for the lowest classes, 2–4, whereas they avoided class 6. Similarly, on a broad scale, they also avoided the most rugged classes, 4 and 5, and selected for classes 1 and 3.

Javelina—Our cameras detected 244 javelinas, or 3.20 detections per 100 trap nights. Javelinas were observed at 30 locations, and they co-occurred with mountain lions at 16 of those locations. Javelina was the only major prey species observed at site H4. Within the study site, javelina use of elevation was different from availability ($\chi^2 = 12.037$, $df = 2$, $P = 0.0024$). High elevations were selected for by javelinas, whereas the middle range of elevations was avoided. Javelina use of ecological systems also was different than availability ($\chi^2 = 19.157$, $df = 4$, $P = 0.0007$). They selected for the Lower Montane Riparian ecological system and they avoided the Pine-Oak and the Pinyon-Juniper systems. On both a broad scale ($\chi^2 =$

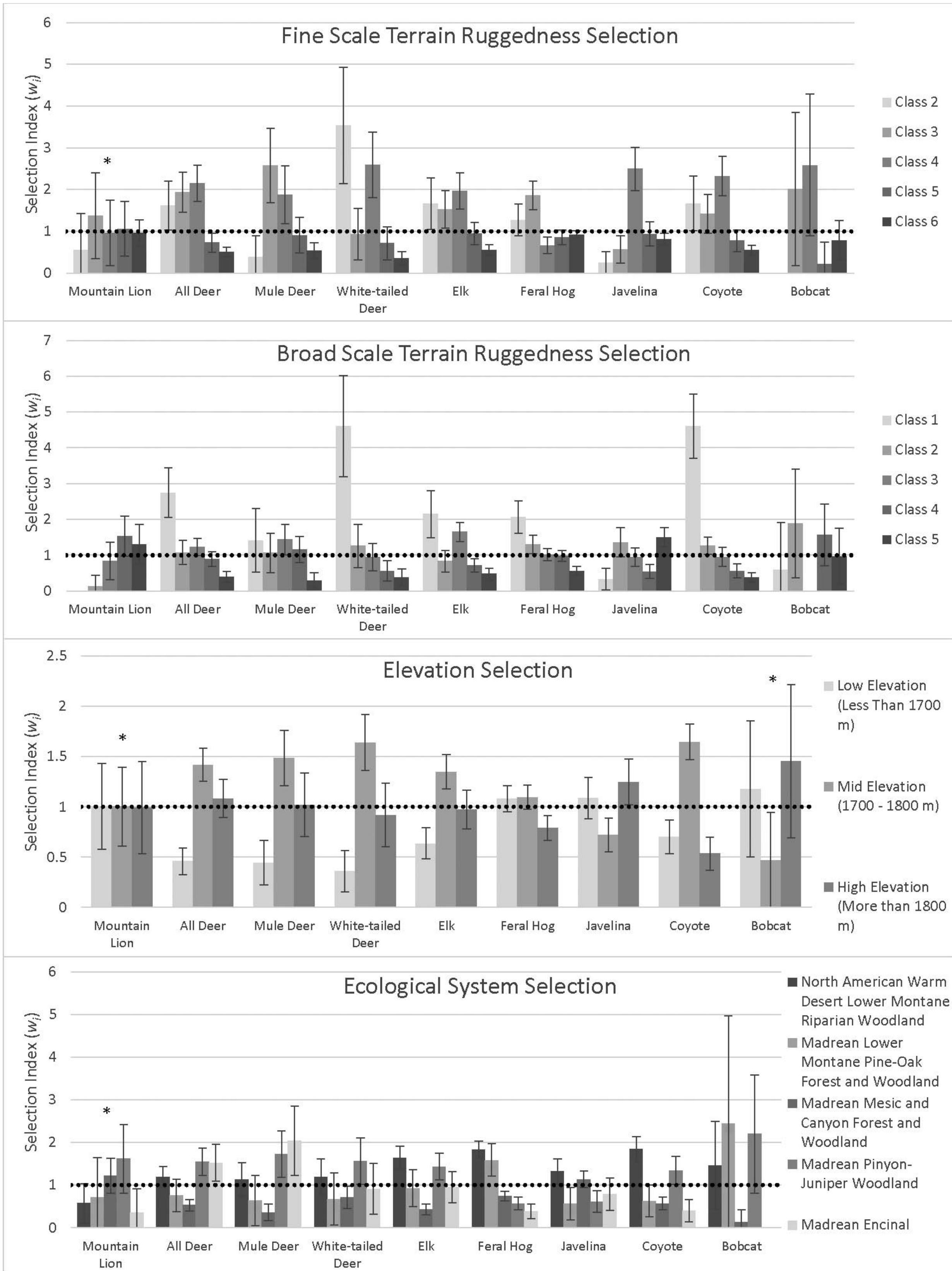

FIG. 2—Habitat selection by species according to terrain ruggedness (fine and broad scale), elevation, and ecological system in the Davis Mountains, Texas, from June 2012 through March 2013. Terrain ruggedness classes range from least to most rugged. Graphs show the selection index (w_i), with 95% confidence intervals. Selection indices with confidence intervals that do not overlap 1 (shown on each graph by a dotted line) were significantly selected (>1) or avoided (<1). Asterisks (*) indicate use of all habitats was in proportion to availability at $\alpha = 0.05$.

43.220, $df = 4$, $P < 0.0001$) and fine scale ($\chi^2 = 92.948$, $df = 4$, $P < 0.0001$), their use of terrain ruggedness classes was different than availability. On a broad scale, they selected for the most rugged terrain, class 5, and avoided classes 1 and 4. On a fine scale, they selected for the middle, class 4, and avoided classes 2, 3, and 6.

Aoudad—Aoudad was the least abundant large prey species we observed, with six detections in total and 0.08 detections per 100 trap nights. They were observed at two locations: H8, located at an elevation of 1,804 m on the edge of the deepest canyon in the study area; and D23, the highest of all of the camera locations, located at an elevation of 2,461 m. Aoudad co-occurred with mountain lions at one location. We did not calculate habitat selection indices for aoudad due to low sample size.

Livestock—Cattle and equines (horses and mules) were the only domesticated species that we included in the "main prey" category. We detected 148 cattle (1.94 detections per 100 trap nights) and 7 equines (0.09 detections per 100 trap nights). Both prey types were detected at two sites (cattle at sites H13 and D9 and equines at sites H13 and H2). Site H13 was located within the main livestock pasture on one of the private ranches; and with the exception of one cattle detection and one equine detection, all livestock detections occurred at this site. Mountain lions were not observed at site H13 during this study, but they were observed at sites D9 and H2.

Predators—Aside from mountain lion, coyote and bobcat were the main predator species in the Davis Mountains. Coyotes and bobcats also make up part of the prey base available to mountain lions. Coyotes were the most abundant predator, with 3.61 detections per 100 trap nights. Bobcats were observed at relatively low numbers, with 0.30 detections per 100 trap nights. Coyotes were the most widespread large predator, observed at 27 sites and co-occurring with mountain lions at 15 of those sites. Bobcats were observed at 10 sites and co-occurred with mountain lions at six of those sites.

Distribution of predators differed by site, and three sites did not yield any photos of large predators (D18, D11, and D13). Several differences were observed between the habitat selection of coyotes and bobcats in the study area. Use of elevation ranges was in proportion to availability for bobcats ($\chi^2 = 4.036$, $df = 2$, $P = 0.1329$), but it differed from availability for coyotes ($\chi^2 = 68.224$, $df = 2$, $P < 0.0001$). Coyotes selected for the mid-range elevations and avoided all others. Both coyote ($\chi^2 = 87.206$, $df = 4$, $P < 0.0001$) and bobcat ($\chi^2 = 17.762$, $df = 4$, $P = 0.0014$) use of ecological systems was significantly different from availability. Coyotes selected for the Pinyon-Juniper and Lower Montane Riparian ecological systems and avoided all others. In contrast, bobcats did not significantly select for any ecological systems, but they did avoid the Mesic and Canyon system. On a fine scale, coyote ($\chi^2 = 109.033$, $df = 4$, $P < 0.0001$) and bobcat ($\chi^2 = 15.05$, $df = 4$, $P = 0.0046$) use of terrain ruggedness was significantly different from availability. Both species showed avoidance of the more rugged classes: bobcats avoided class 5 and coyotes avoided class 6. Coyotes also selected for the less rugged classes 2 and 4. Use of broad-scale terrain ruggedness classes was also significantly different from availability for both bobcats ($\chi^2 = 10.424$, $df = 4$, $P = 0.0339$) and coyotes ($\chi^2 = 325.97$, $df = 4$, $P < 0.0001$). Bobcats only avoided level 3 of broad-scale terrain ruggedness. Similar to the fine scale, on a broad-scale coyotes selected for the least rugged areas, class 1, and avoided the most rugged areas, classes 4 and 5.

Discussion—Feral hogs were the most abundant and widespread major prey species observed in this study. Feral hogs are thought to have been introduced into Texas late in the 17th century, but according to historical surveys were not recorded in the far western part of the state until the 1990s (Taylor, in litt.). Over the past 30 yr, they have quickly become established in the Davis Mountains, as evidenced by their abundance in this survey. Studies of feral hogs in Texas suggest there is the possibility of them competing with native ungulates for resources (Everitt and Alaniz, 1980; Ilse and Hellgren, 1995). In our study site, feral hogs exhibited selection similar to white-tailed deer on a broad scale and to mule deer on a fine scale. Feral hogs also selected for the same Lower Montane Riparian ecological system as elk, and feral hogs and elk both selected for the same levels of fine- and broad-scale terrain ruggedness as well. However, feral hog selection differed from javelina selection across all categories, and feral hog was the only species that selected for the Pine-Oak ecological system. Further research should build upon our initial findings to determine the potential impacts of feral hogs on native species and biodiversity in the Davis Mountains.

Although hogs were found in large numbers, they avoided high elevations and high levels of terrain ruggedness on a broad scale. Coyotes exhibited similar tendencies, avoiding high elevations and terrain ruggedness. However, other species, such as javelina, did select for the more rugged and high-elevation areas that hogs and coyotes avoided. This suggests there might be habitat partitioning by prey in the study area. Based on optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966) and the generalist nature of mountain lions, we would expect to find feral hogs to be the main prey of mountain lions in the area. However, variations in habitat selection by prey and the habitats available within the home ranges of individual mountain lions might result in differences in the prey distribution available to each individual.

Our analysis of resource selection was focused on single elements (i.e., elevation, ecological site, or terrain ruggedness). Although this approach provides important basic knowledge for understanding how a species makes use of the landscape, understanding the combined roles of multiple habitat variables can be important in delineating the niche of a particular species (Hirzel and Le Lay, 2008). Further research could address the question of which habitat characteristics are most important for habitat selection by these species, and how the various habitat characteristics contribute to determining what areas mountain lions and their prey prefer. For example, previous studies have focused on the use of VRM measurements on a fine scale to evaluate habitat suitability (e.g., Sappington et al., 2007). However, the results of our study suggest that looking at broad-scale terrain ruggedness can provide more information on differentiating between habitat preferences for some species. Mountain lions, in particular, only demonstrated use of habitat that was significantly different from availability in the broad-scale terrain ruggedness category, possibly because mountain lions occupy large home ranges, so the immediate habitat is less important than the overall location.

With the exception of broad-scale terrain ruggedness, mountain lion use of all the resource criteria that we evaluated was in proportion to availability. Recent research on mountain lion habitat selection across several sky island mountain ranges in Arizona found consistent selection for woody vegetation (Nicholson et al., 2014). All of the ecological systems that we evaluated in this study typically include woody vegetation, which might account for the lack of significant difference between use and availability in ecological systems. The lack of significant selection exhibited by mountain lions within the study site could be indicating that the entire area we were surveying is adequate habitat for mountain lions, or that factors other than those that we tested are determining habitat use for mountain lions.

Mountain lions avoided the class 2 of broad-scale terrain ruggedness that feral hogs selected. However, feral hogs were observed at all but one location that mountain lions were observed, indicating that mountain lions still could be in a position to prey substantially on feral hogs. Based on studies of mountain lions in similar areas, we would expect mule deer to be an important prey species in the Davis Mountains (Logan and Sweanor, 2001), and mountain lions did not avoid any of the habitat types that mule deer selected, which supports this expectation. However, with the exception of broad-scale terrain ruggedness and feral hogs, mountain lions used all of the habitat types that each major prey species selected, so predation patterns within the study area could be influenced more by overall availability of prey, or other factors such as prey preference of individual mountain lions.

Our results indicate the importance of considering the broad-scale habitat characteristics of an area in addition to the immediate habitat when assessing use of resources. In addition, this study provides valuable knowledge of habitat use by prey species in the Davis Mountains, knowledge that can be combined with mountain lion predation data to form a better understanding of which factors determine mountain lion diet in an ecosystem where a variety of prey are available.

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