

HABITAT USE AND PREY SELECTION BY MOUNTAIN LIONS IN AN ALTERED
SAGEBRUSH STEPPE ENVIRONMENT

By

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ABSTRACT

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Throughout the American West there is an increasing trend of encroachment of woody vegetation on previously open sagebrush steppe habitat. The Modoc Plateau in northeastern California has not been excluded from this encroachment trend and has seen an increase in western juniper (*Juniperus occidentalis*) densities, likely as a result of long-term fire suppression. Mountain lions (*Puma concolor*) have not previously been studied on the Modoc Plateau, and there is potential for an increase in cover due to juniper encroachment to benefit the hunting behavior of lions. To better understand if the presence of cover is being selected by mountain lions, 17 mountain lions were captured and fitted with GPS collars and their movements and diet were monitored. Using remotely obtained location data, I investigated spatially aggregated clusters of GPS points in search of mountain lion feeding sites and their associated kill sites. I created resource selection functions at both the study area and home range levels to test if lions were killing their prey in areas with higher ambush cover, or rather in areas with higher prey densities. Lions spent more time within parts of their home ranges that had larger western juniper basal area. For killing prey, lions selected

areas with increased ambush cover and increased prey densities, compared to what was available within the study area. At the home range level, there was model uncertainty and no selection was observed. At a fine scale, lions selected for areas with more obstructed horizontal visibility, but showed no preference for areas closer to western junipers when killing prey. In areas with declining ungulate populations, there is potential for habitat to be managed by reducing the areas where ungulates are at risk to predation by lions. Through timber cuts and controlled burns, managers have the ability to restore the sage-steppe habitat and reduce areas where ungulates are at greater risk to mountain lion predation.

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TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iv
LIST OF TABLES.....	viii
LIST OF FIGURES.....	x
LIST OF APPENDICES.....	xi
INTRODUCTION.....	1
MATERIALS AND METHODS.....	8
Study Area.....	8
Study Design.....	11
Capturing and collaring.....	11
Home ranges.....	11
Locating kill sites and points of first contact.....	13
Coarse scale habitat selection.....	17
Fine scale habitat selection.....	20
Habitat variation across kill sites by prey species.....	23
RESULTS.....	24
Home Ranges.....	24
GPS Clusters and Diet.....	30
Coarse Scale Habitat Selection at the Study Area Level.....	33
Coarse Scale Habitat Selection at the Home Range Level.....	36
Fine Scale Habitat Selection.....	40
DISCUSSION.....	49

Home Ranges	49
Diet Composition	50
Coarse Scale Habitat Selection	53
Fine Scale Habitat Selection	56
Habitat Variation across Kill Sites by Species	58
Management Implications.....	60
LITERATURE CITED	65
Appendix A.....	76
Appendix B	78
Appendix C	85
Appendix D.....	86

LIST OF TABLES

- Table 1. Home range sizes of adult mountain lions in the study area, located in Modoc and Lassen counties, CA. Home ranges represented as 50%, 85% and 95% kernel density estimates (KDE) recorded in km². Adult females are indicated by the letter F and adult males are indicated by the letter M in the Lion IDs. Means are represented \pm SE..... 25
- Table 2. Frequency and percentage of prey items found at 293 GPS clusters investigated for mountain lions in Modoc and Lassen counties, CA. Species are listed in descending order from most to least frequently found. For the percentage of diet, the GPS clusters where I did not detect prey items were excluded. For the birds category, I combined *Sialia* (n=1), California quail (*Callipepla californica*) (n=3), mourning dove (*Zenaida macroura*) (n=2), red-tailed hawk (*Buteo jamaicensis*) (n=1), sooty grouse (*Dendragapus fuliginosus*) (n=2) and *Picidae* (n=1). The small rodents category combined Belding's ground squirrel (*Uroditellus beldingi*) (n=1), dusky-footed woodrat (*Neotoma fuscipes*) (n=1), and an unknown specimen from the family *Muridae* (n=1). KS = Kill Site; PFC = Point of First Contact. 31
- Table 3. Coarse scale model selection results at the study area level for the prediction of kill sites from mountain lion GPS clusters in Modoc and Lassen counties, CA. The three models with support from the initial model selection were combined to form the combined models 1 and 2, to see if they outperformed the separate hypotheses. 34
- Table 4. Coarse scale beta estimates, odds ratios, and 95% confidence intervals for the parameters of the supported top two models for predicting presence of kill sites at the study area level for mountain lions in Modoc and Lassen counties, CA..... 35
- Table 5. Coarse scale model selection results at the home range level for the prediction of kill sites from GPS clusters of mountain lions in Modoc and Lassen counties, CA. The 4 models with support from the initial model selection were combined to form the combined 1, 2, & 3 models to see if they outperformed the separate hypotheses. 38
- Table 6. Coarse scale beta estimates, odds ratios, and 95% confidence intervals for the parameters of the supported top three models for predicting presence of kill sites at the home range level for mountain lions in Modoc and Lassen counties, CA. 39
- Table 7. Fine scale model selection results for prediction of kill sites. Models were trained using data from the subset of fine scale data measured at kill sites and paired random locations for GPS collared mountain lions in Modoc and Lassen counties, CA. 42
- Table 8. Fine scale model selection results for predicting of points of first contact (PFC) for GPS collared mountain lions in Modoc and Lassen counties, CA. Models were trained

using data from the subset of fine scale data measured at points of first contact and paired random locations. Due to small sample size (n= 15 PFC, n=15 random), fewer predictors were used in PFC candidate models than in kill site candidate models..... 44

Table 9. Mean values for the predictor variables at the kill sites from GPS clusters of mountain lions in Modoc and Lassen counties, CA, for each of the prey species..... 46

LIST OF FIGURES

- Figure 1. Study area boundary shown within northeastern California. The study area encompassed all of Modoc County and the northern portion of Lassen County. Mountain lions were collared and tracked within the bounds of this study area from February 2016 through August 2018..... 10
- Figure 2. The median values of live conifer density for 3 kernel density estimate sizes (50, 85, and 95%) of the 14 GPS collared adult mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, and the minimum and maximum represented by the vertical lines. 27
- Figure 3. The median values of canopy cover for 3 kernel density estimate sizes (50, 85, and 95%) of the 14 GPS collared adult mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, and the minimum and maximum represented by the vertical lines. 28
- Figure 4. The median values of western juniper basal area for 3 kernel density estimate sizes (50, 85, and 95%) of the 14 GPS collared adult mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, the minimum and maximum represented by the vertical lines, and outliers represented by a dot. 29
- Figure 5. A map of kill sites that were observed by backtracking from GPS clusters generated by GPS collared mountain lions in Modoc and Lassen counties, CA. The kill sites are overlaid on a LEMMA layer, depicting larger values for western juniper basal area in deeper shades of red. 32
- Figure 6. The median values of percent slope for each of the 4 species killed by GPS collared mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, the minimum and maximum represented by the vertical lines, and outliers represented by dots..... 47
- Figure 7. The median values of western juniper basal area for each of the 4 species killed by GPS collared mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, the minimum and maximum represented by the vertical lines, and outliers represented by dots..... 48

LIST OF APPENDICES

Appendix A: A Linear Discriminant Function for Habitat Characteristics at Kill Sites ..	76
Appendix B: Home Ranges and Western Juniper Basal Area	78
Appendix C: An Index of Similarity in Diets among Collared Individuals	85
Appendix D: Prey Selection.....	86

INTRODUCTION

Sagebrush steppe ecosystems are experiencing fragmentation from anthropogenic activities in the form of fences for cattle (*Bos taurus*) grazing, increased human presence and development of infrastructure (Rickard 1985, Davies et al. 2011). The encroachment of junipers (*Juniperus sp.*) on open rangelands is further increasing fragmentation by creating dense pockets of vegetation that can divide prairies and create an increase in total edge habitat (Coppedge et al. 2001). There has been a trend of increasing woody vegetation across the interior northwest United States as a result of reduction in fuels from grazing and a decline in fire frequency due to the cessation of indigenous burnings (Anderson 2018, Miller et al. 1999). In the past, more frequent fires with sufficient fuel loads allowed wildfires to reduce the recruitment of woody vegetation. In addition to the increase in western juniper (*Juniperus occidentalis*) density, the decrease in fire frequency and presence of cattle on the landscape, the Modoc Plateau in northeastern California has seen a reduction in winter browse and an increase in invasive grasses over the past few decades (Clements and Young 1997). Furthermore, juniper encroachment impedes flow and duration of ephemeral streams (Zou et al. 2014) and increases soil erosion (Pierson et al. 2010). Juniper encroachment not only changes the water, soil, and the structure and types of vegetation on the landscape, but has potential to change the way wildlife species use available resources. Large felid ambush predators utilize areas with both high prey density and increased ambush cover for killing their prey (Balme et al. 2007, Davidson et al. 2012). If riparian corridors are attractive to ungulates due to

their vegetative composition, and that vegetation also provides ambush cover, then these areas may attract ambush predators as well.

In large parts of the expansive range of mountain lions (*Puma concolor*, hereafter lions), mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) are primary prey species (Hornocker 1970, Ackerman et al. 1984, Logan and Sweanor 2001, Husseman et al. 2003, Thompson et al. 2009). Lions have a large prey breadth and have been documented feeding on an extensive variety of secondary items (Robinette et al. 1959, Ackerman et al. 1984, Iriarte et al. 1990, Blake 2014, Lowrey et al. 2016), but have seldom been documented killing pronghorn (*Antilocapra americana*) (Engstrom and Maxwell 1988, Ockenfels et al. 1994, Keller et al. 2013) or feral horses (*Equus caballus*) (Greger and Romney 1999, Turner and Morrison 2001). On the Modoc Plateau, mule deer, elk, pronghorn, and feral horses, all occur and may be a prey source to lions. However, mule deer, a primary prey source, have declined on the Modoc Plateau as a result of changes in vegetation (Clements and Young 1997). Prey switching has been documented in lion populations when the primary prey source has declined, and this study aims to evaluate prey selection of lions in light of recent ecological changes (Logan and Sweanor 2001, Rominger et al. 2004). Furthermore, lions have never been studied on the Modoc Plateau and little is understood about their foraging habits in this unique region encompassing dry, high-elevation forests that are being encroached by junipers. Previous studies have shown that habitat selection of prey helps to inform habitat selection of lions (Pierce et al. 1999, Grigione et al. 2006), thus it is important to

understand the distribution of prey species within the study area. Each species of ungulate found on the Modoc Plateau utilizes habitat features in different ways and as a result may experience varying levels of predation risk from lions.

Mule deer and elk show similar patterns of habitat selection, preferring areas in close proximity to water (Ordway and Krausman 1986, Boroski and Mossman 1997) with moderate slopes (Ganskopp and Vavra 1987, Sawyer et al. 2006). Both species typically migrate from higher elevations in the summer to lower elevations in the winter (D'Eon and Serrouya 2005, Sawyer et al. 2007). The manner in which mule deer use edge habitat seems to offer an advantage to stalking predators (Logan and Irwin 1985), and it is likely that this same risk applies to elk (Hernandez and Laundre 2005). Mule deer show preference for meadow riparian habitat, and select for aspen (*Populus tremuloides*) groves when under the competitive pressures of cattle grazing (Loft et al. 1991). Deer and elk could be seeking riparian and mesic habitats with a higher density of over-story for thermal protection and security (Jenkins and Wright 1988). In Modoc, where browse has been reduced by livestock grazing, juniper likely provides forage for ungulates as well (Hubbard and Hansen 1976). If mule deer are spending more time in close proximity to western junipers, they may be more susceptible to attacks by predators, which also utilize western junipers for cover. Mule deer in south-central Idaho were disproportionately at risk to predation by lions in juniper habitat (Altendorf et al. 2001).

Pronghorn thrive best in steppe ecosystems that are continuously shaped by fire and provide subclimax vegetation and a wide variety of shrubs and forbs (Yoakum 1979).

The three essential elements of pronghorn habitat are water, forage, and short vegetative structure (Yoakum 1972). Adult pronghorn are typically found in patches of sagebrush that are shorter than 76 cm, and fawns select grass and forb dominated rangelands (Yoakum 1979). Aerial surveys have recorded pronghorn selecting areas within 6 km of water (Yoakum 1979). Drought conditions may reduce pronghorn recruitment and density (Brown et al. 2006). Pronghorn avoid areas with taller vegetation, which may impair their mobility and increase vulnerability to predation (Goldsmith 1990). In 2013, the non-profit Institute for Wildlife Studies in conjunction with California Department of Fish and Wildlife conducted a study on the mortality of female pronghorn on the Modoc Plateau. Eight of 23 adult pronghorn mortalities were attributed to predation by lions (Institute for Wildlife Studies, unpublished data). It has been suggested that areas within pronghorn home ranges that contain dense vegetation likely provide ambush cover for lions (Ockenfels et al. 1994, Keller et al. 2013).

Little is known regarding how feral horses utilize the landscape on the Modoc Plateau. However, studies in other areas indicate that feral horses use landscape features differently than other ungulate species on the Modoc Plateau. Populations of feral horses in south-central Wyoming showed preference for stream-sides, bog meadows and mountain sagebrush habitats and avoided lowland sagebrush habitats (Crane et al. 1997). Coniferous forests and grasslands were neither avoided nor preferred by feral horses (Crane et al. 1997). Feral horses in Wyoming selected for areas within 4.8 km of water sources and within close proximity (1.6 km) to ridges for cooling (Miller 1983). When

horses were in higher elevation habitats (> 1600 m) that were heavily dominated by pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*), it was suspected that lion predation of foals was higher than in more open habitats at lower elevations (Greger and Romney 1999).

Mountain lions occur and thrive across diverse habitat types from hammock swamp forests in Florida (Belden et al. 1988) to high desert ecosystems of the southwest (Logan et al. 1996). Across this range of habitats, and within their home ranges, they select for vegetation types, terrain, slope, and elevation (Logan and Irwin 1985). In western Colorado, lions have been observed selecting habitats used by preferred prey species and spend more time hunting in those habitat types (Lowrey et al. 2016). Lion home ranges are frequently associated with areas of cover (Seidensticker et al. 1973). While lions stalk their prey, they select habitat features that allow them to approach closely enough to attack (Hornocker 1970). Specifically, lions prefer vegetation characteristics that allow them to remain concealed when approaching and ambushing their prey (Logan and Irwin 1985). Lions select for steep rugged topography (Morrison et al. 2014) and typically avoid areas of slope less than 20% (Logan and Irwin 1985). Because lions select habitat with topography and vegetative cover in which prey are vulnerable, changes in vegetation structure is likely to influence both the availability and vulnerability of prey (Logan and Irwin 1985).

Within preferred types of vegetation and terrain, lions consistently display preference for “edge” habitats (Morrison et al. 2014), being as much as four times as

likely to select edge habitat as compared to open areas (Holmes and Laundré 2006). At a fine scale, lion kill sites had more obstructed horizontal visibility than the surrounding habitat (Blake and Gese 2016). In northwestern Utah and southern Idaho, mule deer were killed more frequently than expected in pinyon– juniper habitat (Laundré and Hernandez 2003). It is possible that western junipers are providing more concealment cover for lions in the form of reduced horizontal visibility, while at the same time creating more edge habitat in sagebrush steppe ecosystems.

Presence of water sources may be another factor influencing how lions use habitat. Large herbivores occur in higher densities in close proximity to water (Thrash et al. 1995), and distribution of prey often helps inform habitat selection by lions (Grigione et al. 2002). A negative correlation between distance to water and lion occupancy was observed in Emas National Park in Brazil (Sollmann et al. 2012). In southern California, home ranges of lions shrank during the dry season, suggesting that both lions and their prey were selecting areas in close proximity to water (Dickson and Beier 2002). Lions have also shown preference for hunting in riparian vegetation (Dickson and Beier 2002). Leading up to the study, California had been experiencing a drought (Mann and Gleick 2015) and the effects of water on prey densities and lion hunting behavior may have been amplified in an area such as the Modoc Plateau, where water sources are limited.

The main objective of this study was to elucidate the habitat characteristics selected by mountain lions for stalking and killing on the Modoc Plateau. I tested four hypotheses about lion habitat use. (1) Forest cover positively influences lion habitat

selection within their home ranges. I predicted that lions would spend disproportionately more time in regions of their home ranges that have higher canopy cover, conifer density and western juniper basal area than in less forested areas. (2) Coarse scale habitat characteristics favorable for ambush attacks influence the locations at which lions stalk and successfully kill their prey. I predicted that lions would kill prey in areas with both high prey density as well as high ambush cover. (3) Fine scale habitat characteristics favorable for ambush attacks influence the locations at which lions stalk and successfully kill their prey. At the fine scale, I predicted kill sites and the places lions first contacted their prey would occur in areas with more obstructed visibility, closer to cover (specifically western junipers and conifers), on steeper slopes, closer to water, in areas with more ground cover and at higher elevations. (4) Habitat preferences of prey influence where they are killed by lions. Because mule deer, elk, pronghorn, coyotes and feral horses typically utilize different habitat types, I predicted that slopes, forest cover, and distance to water would differ at kill sites for each species.

MATERIALS AND METHODS

Study Area

This study was conducted in Modoc and Lassen counties of northeastern California, which are part of the Modoc Plateau (Figure 1). The study area is approximately 23,110 km² and is comprised mostly of public land in the form of California State Wildlife areas, Bureau of Land Management, U.S. Forest Service, U.S. Fish and Wildlife Service land with interspersed patches of private land.

Throughout the Modoc Plateau the major water sources are man-made reservoirs, lakes, rivers, snowmelt runoff fed streams, and wetlands. Most water sources in the study area are a part of the Pit River watershed. The study area receives on average 43 cm of precipitation annually, however the higher elevation Warner Mountains can receive up to 121 cm of precipitation due to additional snowfall. Temperatures range from -11° C in the winter months to 32° C in the summer months (Riegel et al. 2006).

The Modoc Plateau is a series of large table lands sculpted from volcanic lava rock. These large mesas occur throughout Modoc County and are dominated by sagebrush steppe habitat. The dominant grassland species on the Modoc Plateau are introduced cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*). Over the past century, there has been an increase in density of western junipers on these mesas. The largest span of uninterrupted western junipers, covering nearly 1,215

km², occurs on the Devil's Garden Plateau in the northern central portion of the study area (Riegel et al. 2006).

The Warner Mountains run north to south through the eastern portion of the study area and range from 1,219 – 3,019 m in elevation. Plant communities in the lower elevations of the Warner Mountains are sagebrush steppe intermixed with western junipers; the middle elevations of the Warner Mountains are dominated by ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*), intermixed with patches of quaking aspen (*Populus tremuloides*) and white fir (*Abies concolor*). White fir are the dominant tree species at higher elevations, with whitebark pine (*Pinus albicaulis*), lodgepole pine (*Pinus contorta murrayana*), and western white pine (*Pinus monticola*) also occurring (Riegel et al. 2006).

There are many ungulate species on the Modoc Plateau including mule deer, elk, pronghorn, feral horses, domestic cattle, domestic sheep (*Ovis aries*), and feral goats (*Capra hircus*). Black bears (*Ursus americanus*) and lions are the apex predators on the landscape, with potential for black bears to displace lions from carcasses (Murphy et al. 1998). Gray wolves (*Canis lupus*) occupy areas north, west and south of the study area, and radio-collared individuals have been documented in the study area for brief periods of time before returning to Oregon. Other mammals in the study area that are potential prey items of lions include badger (*Taxidea taxus*), beaver (*Castor canadensis*), black-tailed jackrabbit (*Lepus californicus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), brush rabbit (*Sylvilagus bachmani*), western spotted

skunk (*Spilogale gracilis*), western striped skunk (*Mephitis mephitis*) and yellow-bellied marmot (*Marmota flaviventris*).

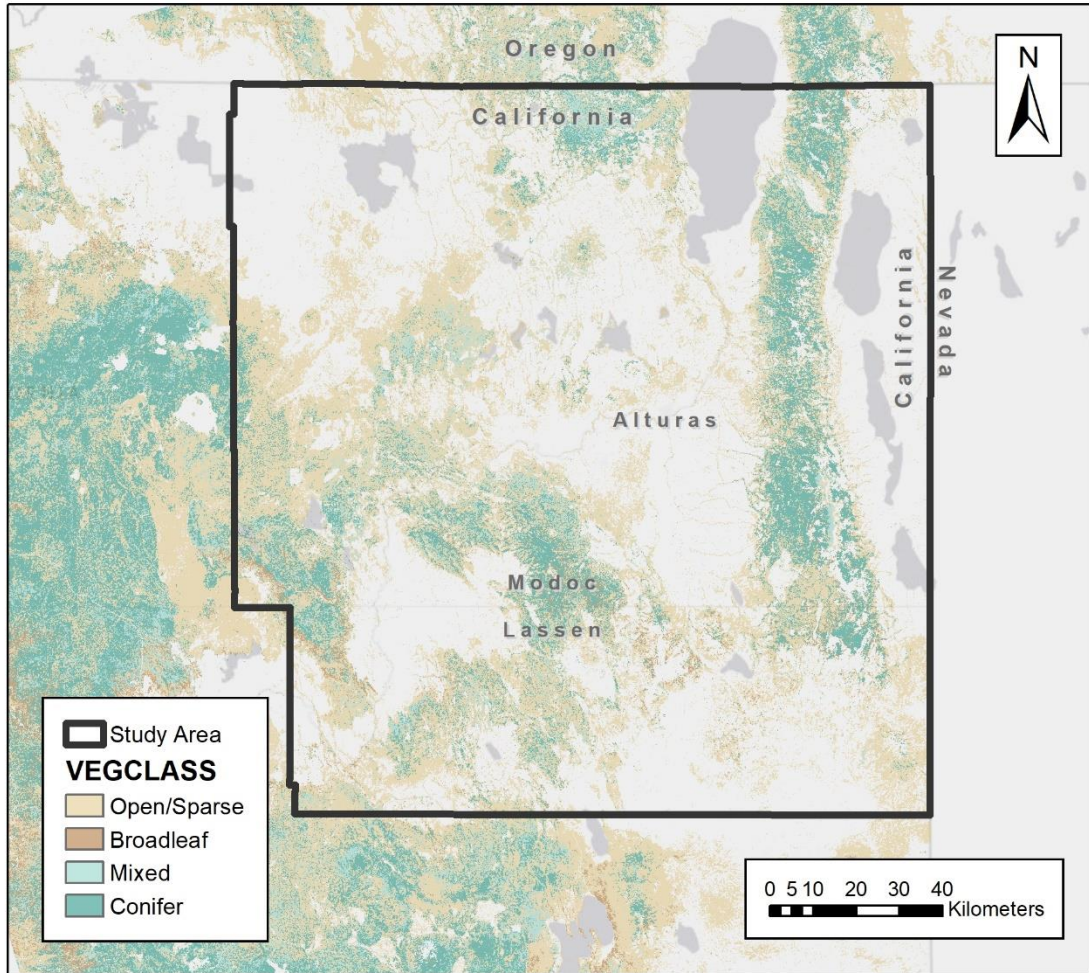


Figure 1. Study area boundary shown within northeastern California. The study area encompassed all of Modoc County and the northern portion of Lassen County. Mountain lions were collared and tracked within the bounds of this study area from February 2016 through August 2018.

Study Design

Capturing and collaring

Lions were captured by the Institute for Wildlife Studies (IWS) between February 2016 and August 2018 for a study on home range sizes and population estimate of mountain lions in the region. Morphometrics of each lion were recorded, and age was estimated based on gum recession of the upper canines and staining of the teeth. Lions were fitted with Lotek Globalstar, Sirtrack Iridium, and Vectronic VERTEX Lite GPS collars. GPS collars were programmed to collect 12 or 24 locations per 24-hour period, and data were uploaded to the Iridium satellite system daily. Each GPS collar was fitted with a timed drop-off mechanism, which allowed the collar to fall off 26 – 90 weeks after attachment to the study animal. Upon retrieval of the collar, data were manually downloaded to acquire points that were not sent through the Iridium or Globalstar networks. Capture and handling procedures were covered under UC Davis' Institutional Animal Care and Use Committee protocol (#18921). All other aspects of the project were covered under Humboldt State University's Institutional Animal Care and Use Committee protocol (16/17.W.97-A).

Home ranges

To test the prediction that lions spend disproportionately more time in forested areas of their home ranges, I first generated home ranges for each individual. I utilized hourly or bihourly locations to generate a 50%, 85% and 95% utilization distribution for each lion. I generated these using fixed kernel density estimates (hereafter KDEs) with

href as the smoothing parameter (Hemson et al. 2005) in package *adehabitatHR* within R Studio version 1.1423 (R Development Core Team 2008, RStudio Team 2016).

To analyze multiple facets of forested areas, so I acquired layers for canopy cover, live conifer density and juniper basal area from the Gradient Nearest Neighbor (GNN) Lemma website (<http://lemma.forestry.oregonstate.edu/data/structure-maps/>). The canopy cover layer was recorded as percent cover, the live conifer density layer was recorded in trees/ha with a diameter at breast height > 2.5cm, and western juniper basal area was recorded in m²/ha within a 30 m resolution. I then utilized the *extract* function in R Studio to obtain values of canopy cover, live conifer density and juniper basal area for each of the 3 home range delineations (50, 85, 95%) for each study animal. Due to the 50% KDE being contained within the larger two delineations, I utilized a donut extraction, which removed the 50% KDE from both the 85% and the 95% KDEs for this analysis.

It has been suggested that kernel density estimates of 95% are of little importance to lions and are prone to errors as a result of smoothing (Seaman et al. 1999), but 85% KDEs show areas of ecological importance to lions and 50% estimations are considered to be core utilization areas (Dickson and Beier 2002). To assess if there was a discernable difference between the “core” areas and the remainder of the areas used by lions, I compared the habitat values from the 50% KDEs to the values from the 85% KDE donuts and the 95% KDE donuts, respectively, utilizing pairwise comparisons. Pairwise

comparisons were made for all 3 habitat variables, and 95% confidence intervals were assessed to see if they overlapped zero.

Locating kill sites and points of first contact

Lions typically move widely across the landscape searching for opportunities to ambush prey; however once cached food is available, they remain in close proximity to the food item (Beier et al. 1995). My first step to locating lion kill sites was to identify spatially aggregated clusters of GPS points (GPS clusters) that may represent where lions were feeding on a large prey item (Beier et al. 1995, Anderson and Lindzey 2003, Elbroch et al. 2014). GPS clusters that occurred more than 1 hour after sunrise and less than 1 hour prior to sunset were considered day beds and not predation events (Elbroch et al. 2013). For my study, GPS locations occurring within 50 m of each other over the course of a 6-hr time span, with at least one point occurring nocturnally, qualified as a GPS cluster (hereafter cluster). Once a GPS cluster was identified, a central point was generated from all of the points within the cluster.

The GPS coordinates of the centroid were then entered into a Garmin GPSMAP 64ST hand held GPS unit. All GPS points were projected in World Geodetic System 1984 and recorded in the Latitude/Longitude coordinate reference system. GPS clusters were prioritized by giving preference to individual lions that had the fewest GPS clusters previously investigated, in an attempt to keep the sampling effort as uniform as possible across individuals.

I hiked to the centroid of GPS clusters and searched for a carcass. If no evidence of hair, blood, bone, rumen or the carcass of a prey item was detected, I systematically searched the area. To ensure that equal search effort was conducted at each GPS cluster investigation, I searched in 10 m concentric rings around the center of the cluster out to a 100 m diameter (Blake 2014).

When carcasses were detected, I recorded the GPS location, the species, age, and sex of prey items, where possible. Mule deer were aged by tooth eruption and categorized as neonates, juveniles, or adults (Pierce II et al. 2011). Horses were also aged based on tooth eruption (American Association of Equine Practitioners 1966). Coyotes were aged by tooth eruption and classified into 2 age classes: juveniles (milk teeth present) and adults (milk teeth replaced) (Nellis et al. 1978). For carcasses that were sufficiently fresh, I searched for canine punctures with any associated hemorrhaging and recorded the maximum width of the punctures. These measurements were used for comparison to known canine widths of captured lions to help determine if it was most likely that the prey item was killed by the collared lion associated with the cluster.

Lions frequently drag their prey from the kill site to nearby vegetative cover, and cache it with sticks, leaves and rocks (Musgrave 1926). From the carcass site I backtracked, following tracks, hair, blood, and drag trails in an attempt to locate the site where the prey was killed by the lion. Characteristic signs of a kill site included, but were not limited to: a large area of disturbed dirt or vegetation, overturned rocks, broken branches, heavily planted prey tracks, large swaths of hair removed from the prey, or

blood (Robinette et al.1959). I only designated a location as a kill site if it contained at least three of the aforementioned characteristics.

Not all prey items are killed at the exact site where a lion abandons its cover and begins to pursue the prey, and there are instances where lions can be shaken off the backs of their prey (Musgrave 1926). I considered the location where a lion first made contact with its prey item the “point of first contact”. Tracking beyond the kill site, I looked for signs of contact such as small isolated clumps of hair, drops or pools of blood and disturbed vegetation without evidence of a drag trail. I identified an area as the point of first contact if I detected any 3 of the following elements beyond the kill site at the end of the drag trail: blood, lion hair indicating a struggle, prey hair, or tracks indicating the lion came into contact with the prey. I acknowledge that for some predation events the kill site and point of first contact may be the same location, and therefore there were inherently fewer points of first contact than kill sites.

Although most feeding events of lions are results of predation, some studies have shown that scavenging occurs as well (Musgrave 1926, Bauer et al. 2005, Elbroch and Wittmer 2013, Elbroch et al. 2014). If I did not find conclusive evidence that a lion killed the prey item, the feeding event was recorded as a “non-predation”. The cause of death for each carcass detected at a GPS cluster was categorized as lion kill, probable lion kill, non-predation, or unknown. Carcasses were classified as lion kills when I observed hemorrhaging in the canine punctures on the neck and the canine width matched that of a lion, or the spinal cord was severed, as lions frequently kill their prey by these methods

(Musgrave 1926, Hornocker 1970, Pierce and Bleich 2003). If I located a kill site and lion sign such as hair or tracks were detected, the carcass was also categorized as killed by a lion. Carcasses were deemed probable lion kills if there was appropriately spaced canine marks in the neck, but no hemorrhaging found, if the carcass had been consumed in a manner similar to the way that lions feed on carcasses, or when the estimated time of death coincided with GPS location data from that collared individual. If the estimated time of death did not match the time when the lion first visited the carcass, or if more of the carcass was consumed than capable by the collared lion for the amount of GPS locations at the carcass, then the carcass was classified as a non-predation. When I was unable to observe sufficient characteristics to classify the carcass into any of the above categories, the carcass was classified as an “unknown”. For my kill site analyses I only included kill sites found where the prey was classified as a lion kill or probable lion kill. However, for my diet composition I included all prey items, due to lions feeding on the carcasses regardless of whether they killed them or not.

For analyzing prey selection by the study lions, I acquired rough population estimates of prey species from both California Department of Fish and Wildlife and the Modoc National Forest for the study area. Since few data were available for non-ungulates within the study area, I only used population estimates for mule deer, elk, pronghorn, and feral horses. Mule deer (California Department of Fish and Wildlife 2019), elk (California Department of Fish and Wildlife 2018), and pronghorn (California Department of Fish and Wildlife, unpublished data) population data were delineated by

hunt zone, so I only included the hunt zone population estimates that had lion territories within them. For feral horse estimates, I only included the Devil's Garden unit as it was the only horse management unit in which I had lions collared. I added all of these estimates together to get an index of the total number of ungulates available to lions on the landscape. I then calculated the proportion of each species that was available on the landscape, by dividing that species population estimate by the total ungulate population. For my analysis of prey selection, I excluded all non-ungulate prey that I found at clusters. I then divided the number of each species found at clusters by the total number of ungulates I detected at clusters to derive the prey composition in the diet of my study lions. I then compared the proportion of each species available to lions to the proportion that occurred on the landscape, as an index for how lions were utilizing the prey.

Coarse scale habitat selection

When analyzing environmental determinants of habitat and kill site selection of large territorial felids, scale and order of habitat selection are of importance (Davidson et al. 2012). To analyze the areas where lions were killing their prey at a coarser scale, I used the full set of kill sites (n=100), and paired random locations (n=100), as habitat variables could be extracted remotely from GIS layers. In addition to looking for differences between fine and coarse scale selection of kill sites, I also wanted to see if there was a difference between the orders of habitat selection (Johnson 1980). For the coarse scale analyses, I elected to look for differences between what was available to lions both at the study area level (2nd order; Johnson 1980), as well as what was available

for each lion within their own home range (3rd order; Johnson 1980). For analyzing where mountain lions were successfully killing their prey compared to what was available to them, I generated random points utilizing *spsample* function within the *sp* package in RStudio (Manly et al. 2002).

The habitat variables I used for the coarse scale analyses were distance to water, slope, vegetation class, canopy cover, live conifer density, and western juniper basal area. However, after I conducted a Variance Inflation Factor test, I found canopy cover to be correlated with conifer density, so I excluded canopy cover from the analysis to avoid issues with multicollinearity (O'Brien 2007). For distance to water, I acquired both linear and area 2018 TIGER shapefiles from the U.S. Census Bureau, and then merged both of these shapefiles in ArcMap (<https://www2.census.gov/geo/tiger/TIGER2018/>). I then utilized the *dist2Line* function within package *geosphere v1.5-10* in RStudio to calculate the distance from each location to the nearest source of water. Because the Modoc Plateau experiences an arid climate and some water sources were subject to seasonal drying, I compared distance to water from the TIGER lines to the subset of kill sites and paired random locations where I had verified the closest water source. I found there to be no significant difference in distance to water between these two methods ($t_{54} = 0.305$, $p = 0.76$).

To determine slope at each kill site, point of first contact, and paired random location, I acquired a 1/3 arc-second resolution Digital Elevation Model (DEM) layer from the U.S. Geological Survey website (<http://ned.usgs.gov/>). I then converted this

DEM into a slope raster in ArcMap V10.4.1 utilizing the slope tool within the spatial analyst tool box, and then used the *extract values to points* function to acquire values for slope.

I acquired layers for vegetation class, live conifer density and juniper basal area from the Gradient Nearest Neighbor Landscape Ecology, Modeling, Mapping & Analysis (GNN LEMMA) database (<https://lemma.forestry.oregonstate.edu/data/structure-maps>). The vegetation class layer categorized the vegetation into 11 classes: sparse, open, broadleaf-sapling/pole, broadleaf-small/medium/large, mixed-small/medium, mixed-large/giant, conifer-saplings/pole, conifer-small/medium, conifer-large, and conifer-giant. The live conifer density layer was recorded in trees/ha with a diameter at breast height > 2.5 cm; western juniper basal area was recorded in m²/ha within a 30 m resolution. Values were obtained for these 3 GNN LEMMA layers by using the *extract values to points* function within ArcMaps V10.4.1 for both kill sites and paired random locations.

I ranked the candidate models with each of the predictor variables separately. I included vegetation class (Clements and Young 1997), distance to water (Boroski and Mossman 1996), and slope (Sawyer et al. 2006) for prey density models. I included live conifer density and western juniper basal area (Carpenter 1998). I chose to be more lenient for the first round of model selection and used a delta AICc <4.0 as a cutoff. If there was support for both prey density and ambush cover models, I combined the top models from each of these categories and re-ran the AICc model selection to assess if the combined model outperformed the models where the predictors were kept separate. For

this second round of model selection, I followed the traditional method of using a delta AICc <2.0 as a cutoff (Burnham and Anderson 2002). When the top model was a combined model, it indicated that lions may have been selecting for both prey density and ambush cover factors.

I did not conduct coarse-scale habitat analyses at the few points of first contact due to coarseness of raster layer cell size and small sample size.

Fine scale habitat selection

I measured fine scale habitat characteristics at a subset of kill sites and points of first contact. To obtain a biologically relevant distance for paired random points, I calculated the mean step length between a cluster centroid and the GPS location prior to the start of the cluster for 10 clusters for each collared lion and calculated the grand mean of these values. This analysis resulted in paired random locations being located 500 m at a random azimuth from kill sites and points of first contact.

I measured 9 habitat characteristics at kill sites (n=55), points of first contact (n=15) and paired random sites (n=55 and 15, respectively). At each location I utilized a measuring tape to record the distance from the center of the site to the nearest available cover, which I defined as vegetation, topography, rocks, or any other structure that was \geq 70 cm in height (approximate shoulder height of an adult lion). I recorded the type (rock, herbaceous vegetation, sagebrush, bitterbrush (*Purshia tridentata*), manzanita (*sp*), mountain mahogany (*sp*), juniper, fir, or pine) of the nearest cover and treated this as a categorical variable. I also noted if this source of cover was a conifer or not and treated

this as a binary categorical variable. Because it has been reported that lions need to be within 25 m or less to successfully kill their prey (Laing 1988, Holmes and Laundré 2006), I estimated horizontal visibility at mule deer eye height (122 cm) between the center of the site and 25 m away in the 4 cardinal and inter-cardinal directions. I measured obstruction of visibility by recording the number of boxes that were obscured by vegetation on a 70 x 70 cm cover board that was divided into 100 boxes total. I then averaged the 8 measurements of obstructed visibility to obtain one value for each location. Additionally, I measured from the center of the site to the nearest western juniper ≥ 70 cm. To measure the percent ground cover, I divided the location into 4 even quadrants based on the 4 cardinal directions. I attached a measuring tape to a 70 cm tall stake in the center of the site and pivoted around the center point at a distance of 5 m, holding the tape level and estimating the percent ground cover of vegetation that was taller than the tape in each quarter of the resulting circular sampling area.

For each kill site and point of first contact, I was interested in the distance to water, as this could be a factor influencing lion use of habitat. Utilizing the hydrography layer from the 2016 onX Hunt GPS micro SD chip on handheld GPS receivers, I identified the closest source of water, hiked to it, and if upon inspection it still had water in it, I recorded the distance (in m) from that location to the site. If this water source did not contain water, I hiked to the next nearest water source and repeated this process.

I evaluated these fine scale habitat characteristics under a conditional logistic regression framework by creating a Resource Selection Function (RSF) for both kill sites

and points of first contact (Manly et al. 2002). The conditional logistic regression was represented by the equation:

$$\text{logit}(x) = \beta_0 + \beta_1 x_1 + \dots \beta_i x_i + \dots + \text{strata}$$

where $\text{logit}(x)$ represented the probability of a kill site or point of first contact, β_0 represented the intercept, β_i represented the coefficient for the habitat variable x_i , and strata represented the cluster ID, which was how kill sites and points of first contact were paired to their associated random locations. I generated 9 a priori candidate models, with the full model represented by: presence of kill site or point of first contact ~ obstructed horizontal visibility + elevation + slope + distance to western juniper + distance to water + distance to nearest cover + percent ground cover + cover type + conifer cover. I then calculated Akaike Information Criterion corrected for small sample size (AICc) for each of the 9 candidate models, ranked the models by the smallest AICc scores, and chose the top models by using a delta AICc cutoff of 2.0 (Burnham and Anderson 2002). To understand the relationship between kill sites and points of first contact with the predictor variables, I evaluated the odds ratio of the beta coefficients for the top models. I calculated the odds ratios for habitat variables in R Studio with the $\text{exp}(\text{coef}())$ function (R Core Development Team 2008, RStudio Team 2016). To represent the certainty in my odds ratios of habitat variables, I also calculated the 95% confidence intervals in RStudio using the $\text{exp}(\text{confint}())$ function.

Habitat variation across kill sites by prey species

To test the hypothesis that habitat characteristics of kill sites vary between prey species, I compared kill sites of mule deer (n = 67), horses (n = 18), pronghorn (n = 8), and coyote (n = 5). I excluded species for which I had an insufficient sample of kill sites (n < 5). I tested variation across species kill sites in distance to water, slope, live conifer density, and western juniper basal area. I utilized the same layers as in previous analyses. To extract values for each of the kill sites, I utilized the *extract values to points* function within ArcMap V10.4.1. Initially I created a Linear Discriminant Function (LDF) to detect differences in these variables across species (Appendix A). However, due to the imbalance in sample size across prey species, the probability of the LDF predicting the prey to be a mule deer over-powered the other 3 species.

I then analyzed the habitat variables for kill sites using an Analysis of Variance (ANOVA). To conduct this portion of the analysis, I used the function *aov* within the package *stats v3.6.1* in RStudio (R Core Development Team 2008, RStudio Team 2016). I used each habitat variable individually in these 4 ANOVAs with the 4 species as levels. I utilized a post-hoc Tukey's Honestly Significant Difference test to elucidate the differences between species using the *TukeyHSD* function embedded within the *stats v3.6.1* package in RStudio (R Core Development Team 2008, RStudio Team 2016).

RESULTS

Home Ranges

I used GPS data for 14 adult mountain lions (6 females, 8 males) and 3 juveniles (all males). GPS collars collected 111,624 (minimum= 1,951; maximum= 16,788) locations between February 2016 and August 2018. From these GPS locations, home ranges were generated using 50%, 85% and 95% KDEs (Table 1). For females, the 50% KDE ($t_{12} = -3.409$, $P = 0.007$), 85% KDE ($t_{12} = -3.385$, $P = 0.007$) and 95% KDE ($t_{12} = -3.3766$, $P = 0.006$) were smaller than those of adult males.

Table 1. Home range sizes of adult mountain lions in the study area, located in Modoc and Lassen counties, CA. Home ranges represented as 50%, 85% and 95% kernel density estimates (KDE) recorded in km². Adult females are indicated by the letter F and adult males are indicated by the letter M in the Lion IDs. Means are represented \pm SE.

Lion ID	50% KDE	85% KDE	95% KDE
F158	31.78	101.26	160.68
F159	74.49	244.61	366.97
F163	143.99	418.63	660.1
F164	133.96	363.62	529.55
F180	48.74	127.33	196.95
F182	65.28	157.49	219.6
<i>Female Mean</i>	83.04 \pm 18.71	235.49 \pm 53.49	355.64 \pm 82.62
M157	212.15	477.95	645.09
M160	85.89	227.25	350.23
M161	321.2	805.52	1119.75
M166	362.08	990.22	1375.29
M178	444.07	1032.43	1378.75
M179	159.78	453.18	672.18
M181	132.69	395.74	604.22
M184	235.38	644.39	963.46
<i>Male Mean</i>	244.16 \pm 43.40	628.34 \pm 103.01	888.62 \pm 134.50

To assess how lions were establishing their core home ranges, I examined live conifer density, canopy cover, and western juniper basal area within their 50%, 85% and 95% KDEs. Dependent juvenile males were excluded from the home range analysis due to their ranges being reflective of their mother's range, rather than their own. I found no difference in live conifer density between the lions' 50% KDEs (\bar{X} = 4.99 trees/ha, 95% CI for the differences: -37.77 – 27.77) and 85% KDEs, nor was there a difference between their 50% and 95% KDEs (\bar{X} = 1.26, 95% CI for the differences: -38.44 – 40.95) (Figure 2). Similarly, I detected no difference in canopy cover between the lion's 50% and 85% KDEs (\bar{X} = 0.24%, 95% CI for the differences: -1.62 – 2.10), nor their 50% and 95% KDEs (\bar{X} = 0.71%, 95% CI for the differences: -1.79 – 3.22) (Figure 3). However, western juniper basal area was higher in the 50% than in the 85% KDEs (\bar{X} = 0.51 m²/ha, 95% CI for the differences: 0.15 – 0.87) and 95% KDEs (\bar{X} = 0.60 m²/ha, 95% CI for the differences: 0.17 – 1.02) (Figure 4).

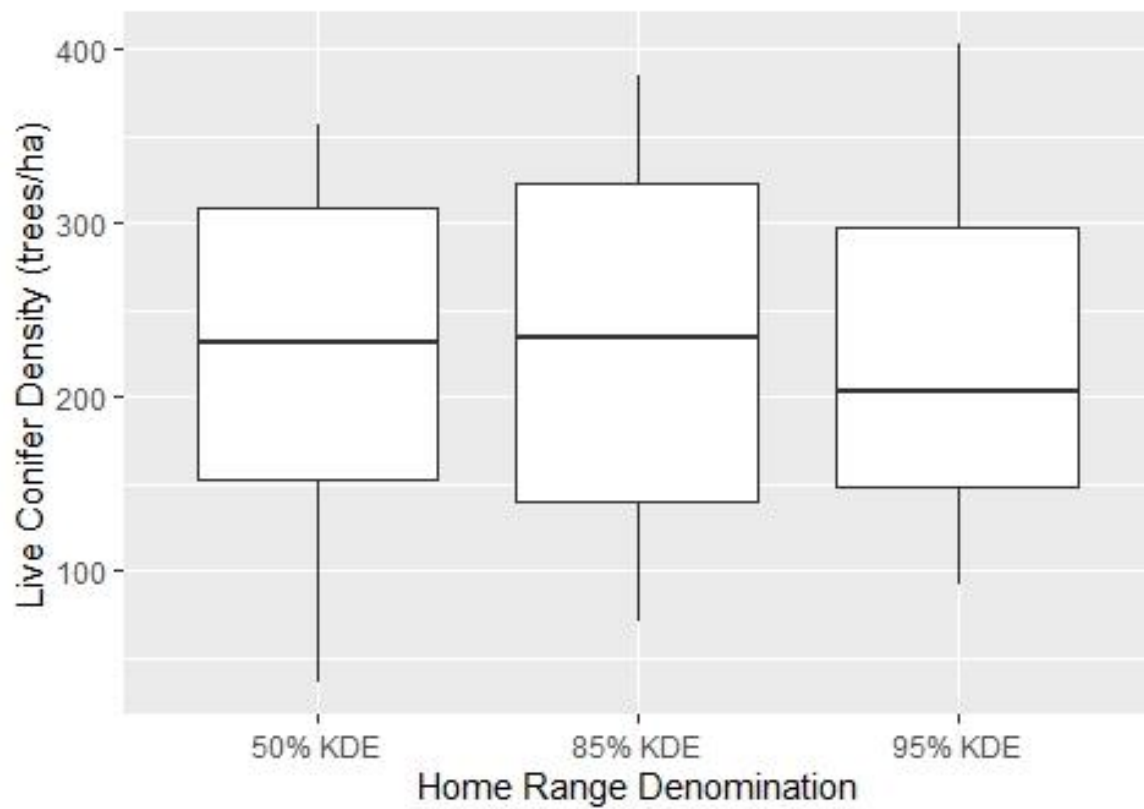


Figure 2. The median values of live conifer density for 3 kernel density estimate sizes (50, 85, and 95%) of the 14 GPS collared adult mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, and the minimum and maximum represented by the vertical lines.

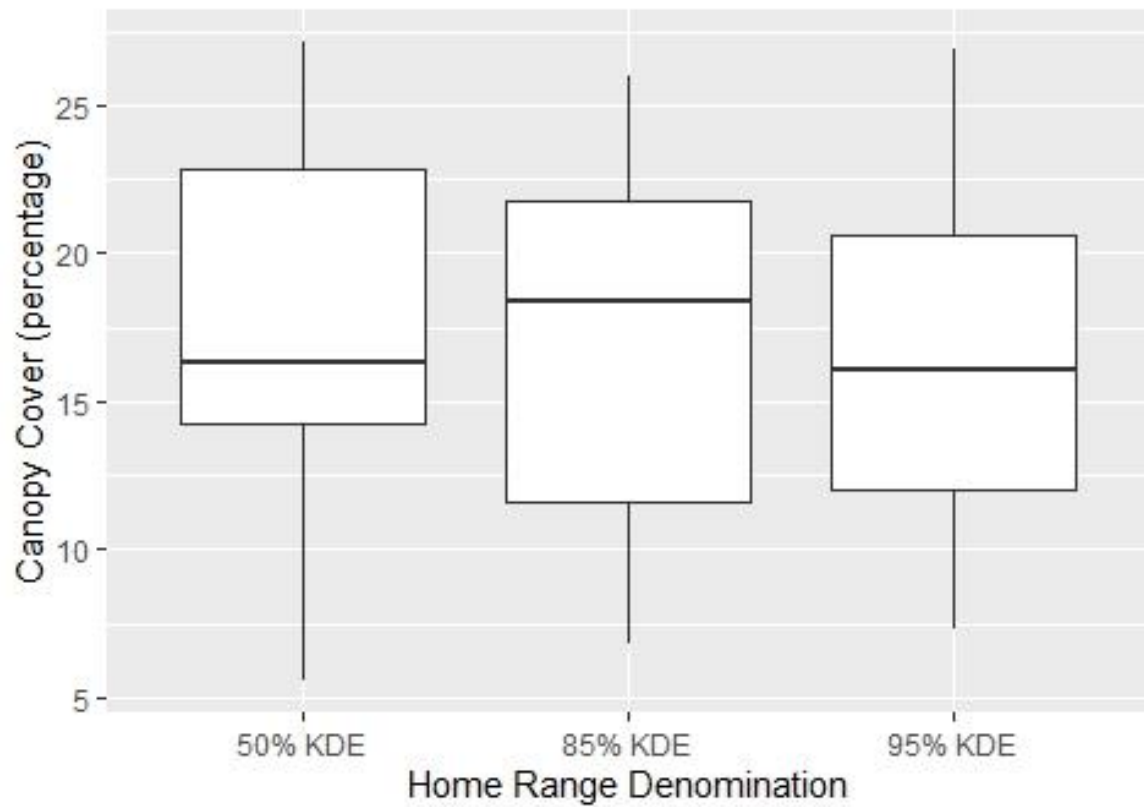


Figure 3. The median values of canopy cover for 3 kernel density estimate sizes (50, 85, and 95%) of the 14 GPS collared adult mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, and the minimum and maximum represented by the vertical lines.

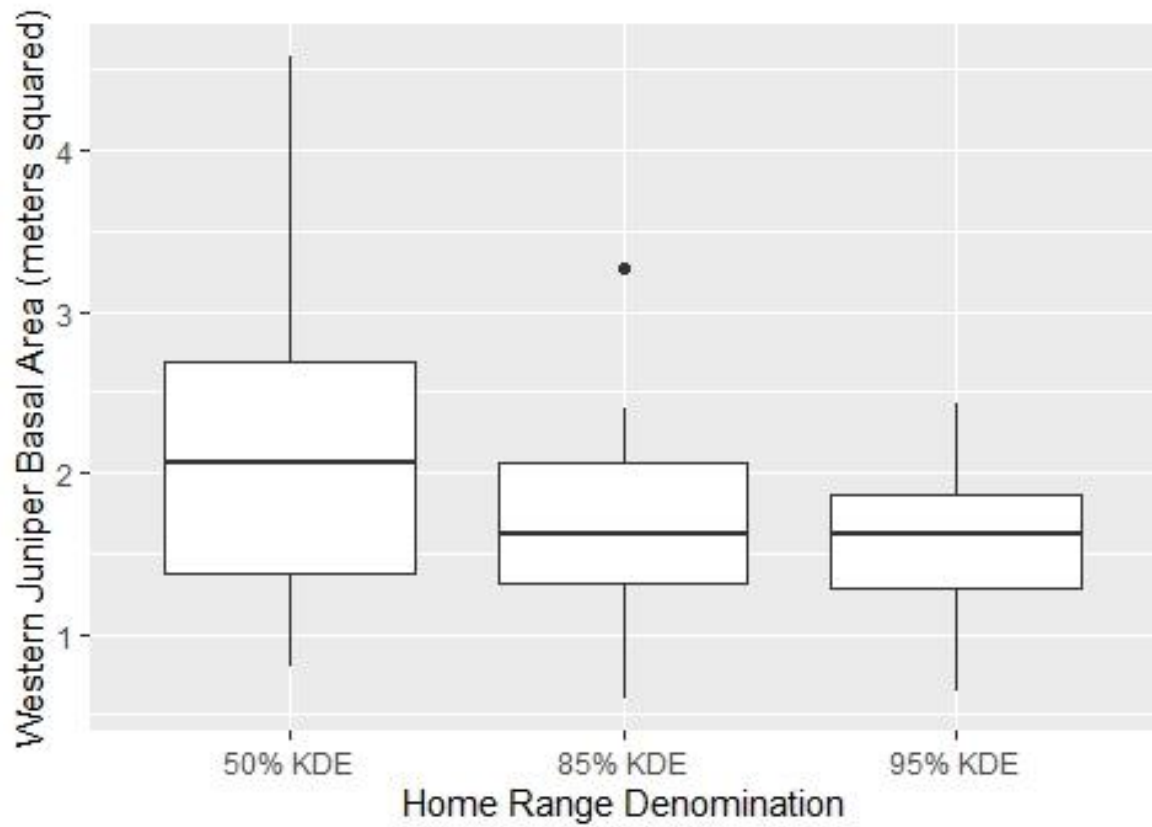


Figure 4. The median values of western juniper basal area for 3 kernel density estimate sizes (50, 85, and 95%) of the 14 GPS collared adult mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, the minimum and maximum represented by the vertical lines, and outliers represented by a dot.

GPS Clusters and Diet

Between April 2016 through August 2018, GPS collar locations were monitored to detect clusters. In total, I investigated 293 GPS clusters from 17 lions (6 adult females, 8 adult males, 3 juvenile males) and detected a prey item at 266 (90.8%) of these sites. Mule deer made up a majority of the prey composition (61.3%), followed by feral horses (10.9%), coyotes (7.5%), birds (4.5%), and pronghorn (3.4%) (Table 2). Out of the 29 feral horses that were observed at GPS clusters, 26 were killed by one individual (M166). Of the 163 mule deer I found at GPS clusters, I was able to determine the sex of 73 (44.8%): 60.3% female and 39.7% males. I determined the age class for 143 (87.7%) of the mule deer: 38 (26.6 %) were fawns, 32 (22.4%) were yearlings, and 73 (51%) were adults. I was able to age 25 of the 29 feral horses (86.2%), of which 96% were juveniles and only one was an adult. I was able to determine the age of 13 of 20 (65%) coyotes, of which pups comprised 15.4%, juveniles comprised 38.5% and adults made up 46.2%. I was unable to determine age class of all birds detected at GPS clusters, due to the limited amount of feathers and carcass remains. I determined age class for 7 (77.8%) of the pronghorn, all of which were adults. Other carcasses that were found less frequently at the GPS clusters included feral goats, cattle, beaver, sheep, small rodents, elk, badgers, brush rabbits, yellow bellied marmot, and feral cat (*Felis catus*) (Table 2). At the GPS clusters that had carcasses of prey items, I was able to identify a kill site at 100 (37.6%) and a point of first contact at 31 (12.4%) clusters (Figure 5).

Table 2. Frequency and percentage of prey items found at 293 GPS clusters investigated for mountain lions in Modoc and Lassen counties, CA. Species are listed in descending order from most to least frequently found. For the percentage of diet, the GPS clusters where I did not detect prey items were excluded. For the birds category, I combined *Sialia* (n=1), California quail (*Callipepla californica*) (n=3), mourning dove (*Zenaida macroura*) (n=2), red-tailed hawk (*Buteo jamaicensis*) (n=1), sooty grouse (*Dendragapus fuliginosus*) (n=2) and *Picidae* (n=1). The small rodents category combined Belding's ground squirrel (*Uroditellus beldingi*) (n=1), dusky-footed woodrat (*Neotoma fuscipes*) (n=1), and an unknown specimen from the family *Muridae* (n=1). KS = Kill Site; PFC = Point of First Contact.

Species	n	Percentage of clusters	Percentage of diet	Number of KS found	Number of PFC found
Mule deer	163	55.6	61.3	66	20
Feral horse	29	9.9	10.9	17	10
No prey observed	27	9.2	n/a	n/a	n/a
Coyote	20	6.8	7.5	5	0
Birds	12	4.1	4.5	1	0
Pronghorn	9	3.1	3.4	8	2
Feral goat	6	2.0	2.3	1	0
Beaver	5	1.7	1.9	0	0
Cattle	5	1.7	1.9	0	0
Sheep	4	1.4	1.5	0	0
Elk	3	1.0	1.1	1	0
Small rodents	3	1.0	1.1	0	0
Badger	2	0.7	0.8	1	1
Brush rabbit	2	0.7	0.8	0	0
Bobcat	1	0.3	0.4	0	0
Feral cat	1	0.3	0.4	0	0
Yellow-bellied marmot	1	0.3	0.4	0	0

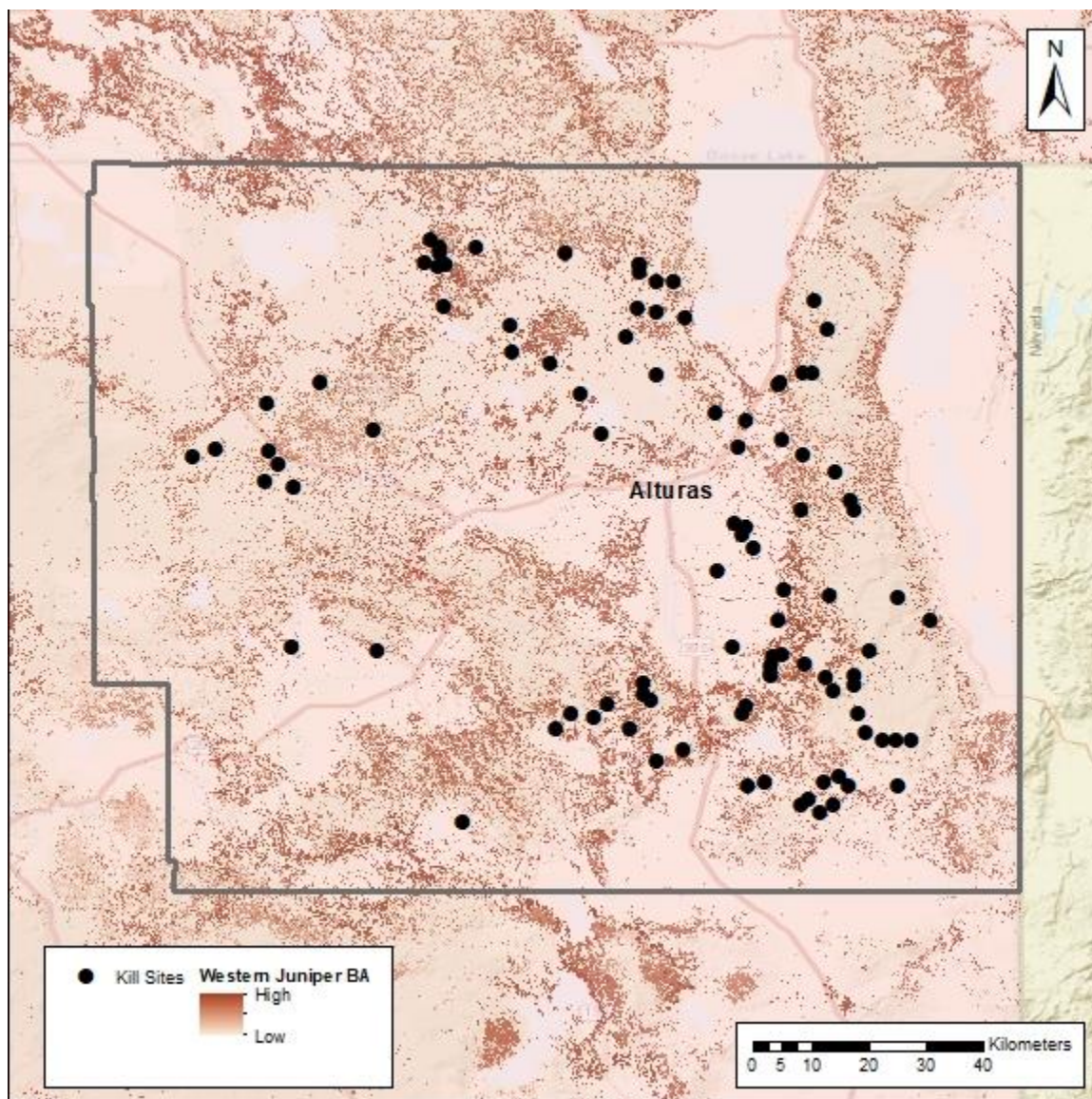


Figure 5. A map of kill sites that were observed by backtracking from GPS clusters generated by GPS collared mountain lions in Modoc and Lassen counties, CA. The kill sites are overlaid on a LEMMA layer, depicting larger values for western juniper basal area in deeper shades of red.

Coarse Scale Habitat Selection at the Study Area Level

To assess habitat selection at all kill sites (n=100) at the study area level, I first compared them to an equal number of random points throughout the study area using a binomial generalized linear model. I tested 2 hypotheses regarding the locations of these kill sites: that mountain lions were killing prey in areas where prey density was high and that mountain lions were killing prey in areas where there was increased ambush cover, with the potential for both of these hypotheses to be supported, but at different scales. I also included a null model, which only included the intercept to test if there was no effect of the predictors.

The top model was ambush 1, which had a weight of 0.614; however, 2 other models carried weight: ambush 3, and prey 1. In order to assess if lions were selecting for both areas with high prey density and high ambush cover, I created 2 new models by combining the top 3 supported models (Table 3). After including the new combined models, the top model was combined 1. For the top model, kill sites were slightly closer to water, slope was slightly steeper, and juniper basal area was larger than at paired random sites (Table 4). There was also support for combined 2 model, which indicated that kill sites were more likely to occur in areas slightly closer to water, with steeper slopes, greater western juniper basal area, and slightly lower conifer densities (Table 4). The models combining predictors from both competing hypotheses outperformed the models that kept the predictor variables separate.

Table 3. Coarse scale model selection results at the study area level for the prediction of kill sites from mountain lion GPS clusters in Modoc and Lassen counties, CA. The three models with support from the initial model selection were combined to form the combined models 1 and 2, to see if they outperformed the separate hypotheses.

Model Name	Model Parameters	df	AICc	Δ AICc	Weight
combined 1	dwater + slope + juniper basal	4	267.7	0	0.588
combined 2	dwater + slope + juniper basal + coniferdens	5	269.5	1.81	0.238
ambush 1	juniper basal	2	271.2	3.42	0.106
ambush 3	juniper basal + coniferdens	3	273.2	5.48	0.038
prey 1	dwater + slope	3	274.2	6.44	0.023
null		1	279.3	11.54	0.002
prey 2	vegclass + dwater	9	279.6	11.83	0.002
prey 4	vegclass + dwater + slope	10	280.6	12.83	0.001
ambush 2	coniferdens	2	281.1	13.33	0.001
prey 3	vegclass + slope	9	282.3	14.59	0.000

juniper basal = the basal area of western junipers in m²/ha

coniferdens = live conifer density measured in trees/ha

dwater = the distance to the nearest water source in m

slope = the slope which was measured in percentage

vegclass = a categorical variable representative of the 11 vegetation classes

prey = indicates that the model is a part of the prey density hypothesis

ambush = indicates that the model is a part of the ambush cover hypothesis

Table 4. Coarse scale beta estimates, odds ratios, and 95% confidence intervals for the parameters of the supported top two models for predicting presence of kill sites at the study area level for mountain lions in Modoc and Lassen counties, CA.

Model Name	Parameter	Beta	Odds Ratio	Lower CI	Upper CI
combined 1	intercept	-0.2343717602	0.791	0.4945877	1.268157
combined 1	dwater	-0.0003623777	0.999	0.9990383	1.000106
combined 1	slope	0.0499986915	1.051	1.0009339	1.109601
combined 1	juniper basal	0.1336187961	1.143	1.0393224	1.304665
combined 2	intercept	-0.2286331094	0.796	0.4972799	1.275675
combined 2	dwater	-0.0003563420	0.999	0.9990458	1.000111
combined 2	slope	0.0540052915	1.055	1.0028155	1.116952
combined 2	juniper basal	0.1367281024	1.147	1.0417103	1.310057
combined 2	coniferdens	-0.0002225546	0.999	0.9988730	1.000600

int = the intercept

juniper basal = the basal area of western junipers in m²/ha

coniferdens = live conifer density measured in trees/ha

dwater = the distance to the nearest water source in m

slope = the slope which was measured in percentage

vegclass = a categorical variable representative of the 11 vegetation classes

prey = indicates that the model is a part of the prey density hypothesis

ambush = indicates that the model is a part of the ambush cover hypothesis

Coarse Scale Habitat Selection at the Home Range Level

To assess habitat selection at kill sites (n=100) at the home range level, I compared them to random points (n=100) generated throughout the lions' home ranges using a conditional logistic regression framework. The number of kill sites detected for each lion was different, so I generated the same number of random points as kills for each lion, and used each lion ID as a stratum. Similar to the study area level RSF, I wanted to test the same 2 hypotheses regarding the locations of these kill sites: that mountain lions were killing prey in areas where prey density was high, and that mountain lions were killing their prey in areas with increased ambush cover, with the potential for both of these hypotheses to be supported, but at different scales. The top model was the ambush 1 model; however, 3 other models carried weight: ambush 2, prey 1, and ambush 3 models. To assess if lions were selecting for both areas with high prey density and ambush cover, I created 3 new models by combining the top 4 supported models. After including the new combined models, the top model was still ambush 1 model, which contained western juniper basal area, but there was also support for ambush 2 and prey 1 models, as in the previous model selection exercise (Table 5). There was weak support for western juniper basal area being slightly higher (Odds Ratio= 1.027873, 95% CI: 0.9861496– 1.071362) at kill sites as compared to paired random points (Table 6). There was also weak support for kill sites occurring in areas of higher conifer density (Odds Ratio= 0.9999446, 95% CI: 0.9996821– 1.000207). The prey 1 model indicated weak evidence of kill sites occurring closer to water (Odds Ratio= 0.9998194, 95% CI: 0.9995826– 1.000056) and

on steeper slopes (Odds Ratio= 1.0032661, 95% CI: 0.9780098– 1.029175) (Table 6).

The models that combined predictors from both hypotheses did not outperform the models that kept the predictor variables separate.

Table 5. Coarse scale model selection results at the home range level for the prediction of kill sites from GPS clusters of mountain lions in Modoc and Lassen counties, CA. The 4 models with support from the initial model selection were combined to form the combined 1, 2, & 3 models to see if they outperformed the separate hypotheses.

Model Name	Model Parameters	df	AICc	Δ AICc	Weight
ambush 1	juniper basal	1	240.7	0	0.299
ambush 2	coniferdens	1	241	0.23	0.267
prey 1	dwater + slope	2	241.6	0.9	0.191
ambush 3	juniper basal + coniferdens	2	242.8	2.08	0.106
combined 1	dwater + slope + juniper basal	3	243.6	2.89	0.07
combined 2	dwater + slope + coniferdens	3	243.8	3.02	0.066
combined 3	dwater + slope + juniper basal + coniferdens	4	245.8	5.06	0.023
prey 3	vegclass + slope	8	253.7	12.91	0
prey 2	vegclass + dwater	8	254.6	13.83	0
prey 4	vegclass + dwater + slope	9	255.7	14.98	0

juniper basal = the basal area of western junipers in m²/ha

coniferdens = live conifer density measured in trees/ha

dwater = the distance to the nearest water source in m

slope = the slope which was measured in percentage

vegclass = a categorical variable representative of the 11 vegetation classes

prey = indicates that the model is a part of the prey density hypothesis

ambush = indicates that the model is a part of the ambush cover hypothesis

Table 6. Coarse scale beta estimates, odds ratios, and 95% confidence intervals for the parameters of the supported top three models for predicting presence of kill sites at the home range level for mountain lions in Modoc and Lassen counties, CA.

Model Name	Parameter	Beta	Odds Ratio	Lower CI	Upper CI
ambush 1	intercept	0.4746395	1.607	1.4079885	1.835133
ambush 1	juniper basal	0.0275	1.028	0.9861496	1.071362
ambush 2	intercept	0.5106386	1.666	1.451501	1.913912
ambush 2	coniferdens	-0.0000554	0.999	0.9996821	1.000207
prey 1	intercept	0.570147269	1.769	1.4180449	2.205635
prey 1	dwater	-0.000180574	0.999	0.9995826	1.000056
prey 1	slope	0.00326	1.003	0.9780098	1.029175

juniper basal = the basal area of western junipers in m²/ha

coniferdens = live conifer density measured in trees/ha

dwater = the distance to the nearest water source in m

slope = the slope which was measured in percentage

vegclass = a categorical variable representative of the 11 vegetation classes

prey = indicates that the model is a part of the prey density hypothesis

ambush = indicates that the model is a part of the ambush cover hypothesis

Fine Scale Habitat Selection

Habitat characteristics were measured at a subset (n=55) of kill sites for the fine scale habitat analysis. Horizontal visibility at kill sites was more obstructed than at paired random points ($t_{54} = 3.73$, $p < 0.001$). Although I found no difference in distance to the nearest western juniper ($t_{54} = 0.53$, $p = 0.60$), distance to nearest cover was significantly shorter at kill sites than at paired random points ($t_{54} = -2.59$, $p = 0.01$). There was no difference in distance to water ($t_{54} = -0.25$, $p = 0.80$), ground cover within a 5 m radius ($t_{54} = 0.79$, $p = 0.43$), or slope between kill sites and paired random points ($t_{54} = -0.92$, $p = 0.36$).

Habitat characteristics were also measured at a subset (n=15) of points of first contact for the fine scale habitat analysis. Horizontal visibility at points of first contact was significantly more obstructed than at paired random points ($t_{14} = 2.38$, $p = 0.03$), and points of first contact occurred significantly closer to cover than paired random points ($t_{14} = -2.7$, $p = 0.049$). I found there to be no difference in the distance to western junipers ($t_{14} = 0.16$, $p = 0.87$), the mean distance to water ($t_{14} = 0.02$, $p = 0.99$), slope ($t_{14} = -0.47$, $p = 0.64$), or ground cover within a 5 m radius ($t_{14} = 1.95$, $p = 0.06$) at the point of first contact when compared to paired random points.

I generated 9 a priori candidate models, with the full model represented by: kill site presence ~ obstructed horizontal visibility + elevation + slope + distance to western juniper + distance to water + distance to nearest cover + percent ground cover + cover type + conifer cover (Table 7). There was support for two models: a model that included

obstructed horizontal visibility (model 1) and a model that included obstructed horizontal visibility, distance to nearest western juniper and distance to nearest cover (model 2). Of these two supported models, I chose the most parsimonious model (model 1) for predicting the presence of kill sites based on fine scale data. For the top model, the obstructed horizontal visibility predictor had a positive effect on presence of kill sites ($\beta = 0.08296$, Odds Ratio = 1.0865, 95% CI: 1.038 – 1.137), meaning that kill sites were more likely to occur in areas where the cover board was more obscured.

Table 7. Fine scale model selection results for prediction of kill sites. Models were trained using data from the subset of fine scale data measured at kill sites and paired random locations for GPS collared mountain lions in Modoc and Lassen counties, CA.

Model #	Model Parameters	df	AICc	Δ AICc	Weight
1	visobs	1	53.5	0	0.505
2	visobs + djun + dcover	3	54.4	0.81	0.337
3	visobs + dcover + dwater	3	55.9	2.36	0.155
4	visobs + dcover + covtype	10	65.2	11.66	0.001
5	visobs + djun + dcover + covtype + conif	12	65.4	11.88	0.001
6	visobs + dcover + dwater + covtype	11	67.5	13.98	0.000
7	visobs+ dcover + dwater + gc + elev + covtype + conif	14	74.9	21.35	0.000
8	visobs + djun + dcover + dwater + gc + slope + elev + covtype + conif	16	75.3	21.76	0.000
9	visobs + dcover + dwater+ gc + slope + elev + covtype + conif	15	76	22.41	0.000

visobs = the percentage of a 0.7 m² cover board that was obstructed from viewing at 25 m in the 4 cardinal and 4 inter-cardinal directions

djun = the distance in m to the nearest western juniper, trees < 0.7 m in height were excluded

dcover = the distance in m to the nearest cover that was ≥ 0.7 m

dwater = the distance in m to the nearest water source

gc = the percent ground cover that was ≥ 0.7 m within a 5 m radius

covtype = a categorical variable representing the nearest type of cover that was ≥ 0.7 m

conif = a binary variable indicating whether the nearest source of cover was a conifer or not

elev = the elevation in m, which was extracted from a Digital Elevation Model

For points of first contact, I generated 8 a priori candidate models, with the full model represented by: point of first contact presence ~ obstructed horizontal visibility + slope + distance to nearest western juniper + distance to nearest water + distance to nearest cover (Table 8). There was support for a single top model, based on its AICc score and majority of weight that it carried. Similar to the fine scale analysis of kill sites, the most parsimonious model included only obstructed horizontal visibility (model 1). The obstructed horizontal visibility predictor had a positive effect on the presence of points of first contact ($\beta = 0.1291$, Odds Ratio = 1.1378, 95% CI: 0.9451 – 1.3699), meaning that points of first contact were more likely to occur in areas where horizontal visibility was more obscured.

Table 8. Fine scale model selection results for predicting of points of first contact (PFC) for GPS collared mountain lions in Modoc and Lassen counties, CA. Models were trained using data from the subset of fine scale data measured at points of first contact and paired random locations. Due to small sample size (n= 15 PFC, n=15 random), fewer predictors were used in PFC candidate models than in kill site candidate models.

Model #	Model Parameters	df	AICc	Δ AICc	Weight
1	visobs	1	14.2	0	0.757
2	distance to cover	1	17.5	3.29	0.146
3	visobs + distance to cover + djun	3	19.3	5.09	0.059
4	slope	1	22.6	8.44	0.011
5	djun	1	23.1	8.91	0.009
6	distance to water	1	23.1	8.94	0.009
7	visobs + distance to water + distance to cover + slope + djun	5	24	9.79	0.006
8	distance to water + slope	2	25.3	11.13	0.003

visobs = the percentage of a 0.7 m² cover board that was obstructed from viewing at 25 m in the 4 cardinal and 4 inter-cardinal directions

djun = the distance in m to the nearest western juniper, trees less than 0.7 m in height were excluded

distance to cover = the distance in m to the nearest cover that was ≥ 0.7 m

distance to water = the distance in m to the nearest water source

Habitat Variation across Kill Sites by Species

The data used for determining differences in kill site characteristics by species included mule deer ($n = 67$), feral horses ($n = 18$), pronghorn ($n = 8$), and coyote ($n = 5$). I found that slope differed between kill sites of different species ($F_3 = 4.196$, $p = 0.008$) (Table 9). I observed that mean slope at kill sites of mule deer was 5.4% steeper than at kill sites of feral horses ($p = 0.005$, 95% CI: 1.307 – 9.496) (Figure 6). I also found a difference in western juniper basal area at kill sites of different species ($F_3 = 3.312$, $p = 0.023$). Pronghorn were killed in areas with western juniper basal area that was 4.8 m² greater than in areas where mule deer were killed ($p = 0.055$, 95% CI: -0.074 – 9.751) (Figure 7). I did not detect significant differences in the mean distance to water ($F_3 = 0.294$, $p = 0.83$) nor in live conifer density ($F_3 = 1.714$, $p = 0.17$) at kill sites across the 4 species (Table 9).

Table 9. Mean values for the predictor variables at the kill sites from GPS clusters of mountain lions in Modoc and Lassen counties, CA, for each of the prey species.

Species	Slope (%)	Distance to water (m)	Conifer density (trees/ha)	Western juniper basal area (m ²)
Mule deer	7.41	429.27	184.96	1.43
Feral horses	2.01	520.08	48.57	1.79
Coyotes	4.86	415.54	370.91	6.09
Pronghorn	4.79	244.09	89.24	6.27

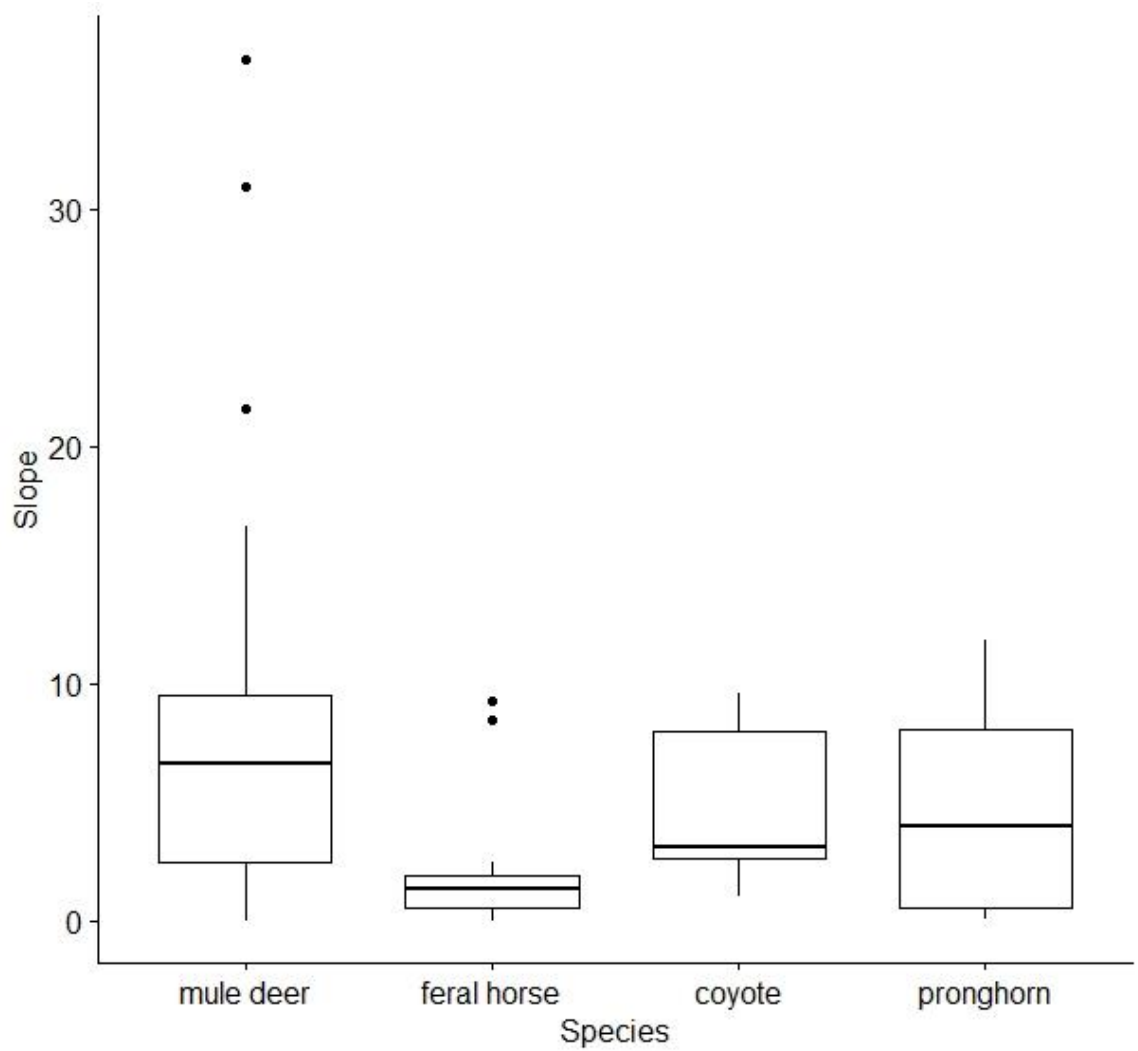


Figure 6. The median values of percent slope for each of the 4 species killed by GPS collared mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, the minimum and maximum represented by the vertical lines, and outliers represented by dots.

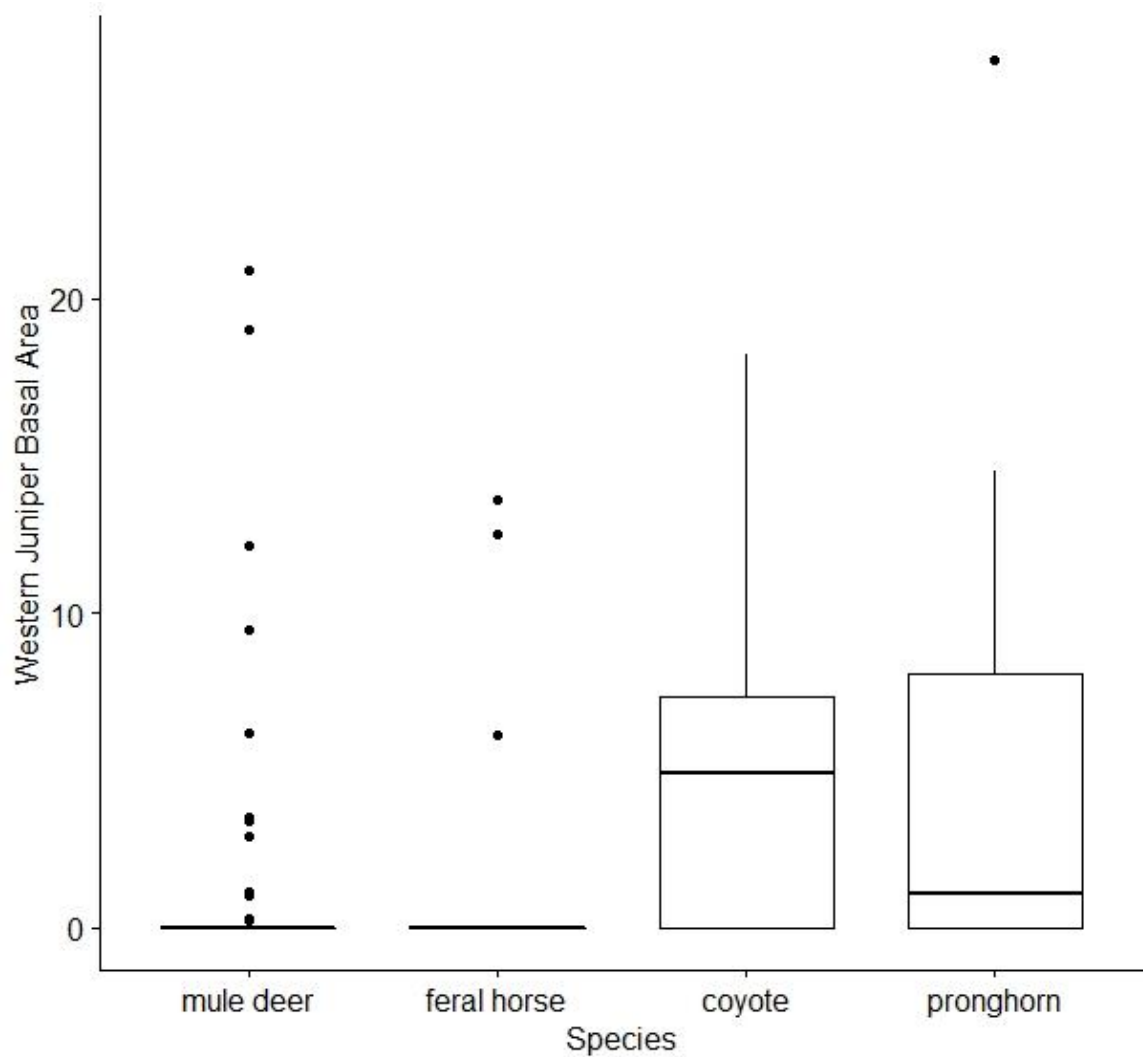


Figure 7. The median values of western juniper basal area for each of the 4 species killed by GPS collared mountain lions in Modoc and Lassen counties, CA between 2016-2018. Interquartile ranges are represented by the boxes around the lines, the minimum and maximum represented by the vertical lines, and outliers represented by dots.

DISCUSSION

Western juniper played an important role in the way lions partitioned their time, as seen by the establishment of their core ranges around juniper with larger basal area. At the coarse scale, lions killed their prey in areas that had steeper slopes and had larger western juniper basal area. At the fine scale, lions killed their prey in areas with more obstructed horizontal visibility.

Home Ranges

Overall, there was high variance among lions in their use of habitat within their home ranges (3rd order habitat selection; Johnson 1980). The entire home range of some lions were in habitat with high values for canopy cover and conifer density. Consequently, this masked detection of differences in live conifer density and canopy cover between the 50%, 85% & 95% KDEs of all the lions sampled. These results suggest that lions may be selecting for forest cover when establishing their home ranges on the landscape (2nd order habitat selection; Johnson 1980).

Although I did not observe differences for canopy cover and live conifer density between core use areas and entire home ranges, lions did show evidence of preferentially using core areas within their home ranges that had higher western juniper basal area (Appendix B). The characteristics of western juniper habitat may benefit lions in a variety of ways. Mountain lions typically drag their prey into areas of more dense cover, which prolongs carcass life (Musgrave 1926). Larger western junipers may have more duff

underneath them for the caching of carcasses. These larger trees are also likely to have more complex branching for concealing their prey items from scavengers. Another reason lions may be using western junipers with larger basal area is for thermal benefit. Western junipers have the potential to act as a thermal buffer for lions, both in the form of shade in summer months and as a shield from the elements in winter months. It is also possible that lions established their core ranges around larger western juniper basal area for increased cover for hunting, as supported by the coarse scale kill site analysis. In theory, fire suppression would allow for later successional stages of western junipers to persist, which would increase areas with trees of larger basal areas. Although my study did not fully elucidate why lions are utilizing these junipers of larger basal area, they appear to be an important habitat characteristic for lions. This was apparent at multiple levels, as juniper basal area was larger within the core of their home range, and at kill sites, both when compared to the rest of the study area and their home ranges.

Diet Composition

I was able to detect prey items at 90.8% of the GPS clusters I investigated. Mountain lions consumed more mule deer (61%) than any other prey items, followed by feral horses, coyote, birds and pronghorn. This supports results from other studies that show lions primarily eat mule deer when most abundant (Pierce et al. 2000, Villepique et al. 2011, Allen et al. 2014). Other studies have shown secondary prey items of lions to include desert cottontails (*Sylvilagus audubonii*) and black-tailed jack rabbits in the

eastern Sierra of California (Pierce et al. 2000), domestic cattle and javelina (*Pecari tajacu*) in southeastern Arizona (Cunningham et al. 1999), javelina and feral hogs (*Sus scrofa*) in southern Texas (Harveson et al. 2000), beaver in western Washington (Kertson et al. 2011) and porcupines (*Erethizon dorsatum*) in northwestern Nevada (Sweitzer et al. 1997). Interestingly, I observed a surprisingly high number of feral horse kills by one male study animal (M166). Within that individual's home range, mule deer densities were lower compared to that of other study animals (California Department of Fish and Wildlife 2019). This is congruent with a study in the Pryor Mountains of Montana, where it was suggested that a single lion was focusing on bighorn sheep as prey as a result of availability within this individual lion's home range (Blake 2014).

A Morasita Horn Index of Similarity analysis found that M166's diet was strikingly dissimilar from that of the other study animals (Horn 1966; Appendix C). When M166 was removed from the diet analysis as an outlier, mule deer comprised 68.4% of the diet, and feral horses comprised less than 1% of the remaining lions' diet. It is likely that not all lions had equal access to all prey types within their home ranges. Only 4 study animals had home ranges that overlapped with horse and burro management units. If I had more animals collared within areas of high feral horse concentrations, there would be potential for feral horses to be hunted by more than just a few lions and emerge as an even larger portion of their diet. It is likely that M166's diet likely reflects the abundance of prey available to him, as horse populations were high within his home range (Appendix D). It is possible that the high number of horses observed in our

sampling is representative of apparent competition occurring between feral horses and other prey species on the Modoc Plateau (Holt 1977).

The number of coyote carcasses detected at GPS clusters was unusually high. Other studies have found that coyotes comprise a low percentage of lion diet in the mountain west (1.8%, Ackerman et al. 1984; 1.97%, Kertson et al. 2011; 3%, Blake 2014) or are not found at all (Leopold and Krausman 1986, Cunningham et al. 1999, and Harveson et al. 2000). In central Idaho, it was suggested that lions may kill coyotes at their feeding sites while defending prey carcasses (Koehler and Hornocker 1991). I acknowledge that mountain lions and coyotes may exhibit intraguild competition (Palomares and Caro 1998), however all of the coyotes I detected at GPS clusters were more than 50% consumed by lions. This led me to believe that lions of the Modoc Plateau may be utilizing coyotes as supplemental food sources to their primary prey of mule deer. Unlike the bias observed with feral horses, coyotes were taken by more than half of the study animals. This may indicate that in areas where primary prey densities are low, lions use coyotes as supplemental food sources.

Initially I anticipated that pronghorn would make up a larger proportion of the lions diet than I observed, due to a congruent study finding lions to be the main predator of collared pronghorn in the area (IWS, unpublished data). Drought may have been a factor in the high mortality observed in that study, which occurred in the severe drought years of 2014-2016 (Funston and Mills 2006). If primary water sources were dry, pronghorn may have had to utilize secondary water sources that were less desirable in

terms of predation risk. Alternatively, GPS collared pronghorn may have been weakened during capture and could have been more susceptible to predation by lions due to capture-related myopathy (Mech 1967). Although high numbers of pronghorn were not detected in my GPS cluster investigations, lions may still have the potential to impact their populations.

Although my cluster parameters (6 hours spent within a 50 m span, with 1 or more nocturnal locations) were more conservative than other lion diet studies (Anderson and Lindzey 2003, Bacon et al. 2011, Blake 2014, Lowrey et al. 2016), I consider them sufficient for the purpose of locating kill sites of large prey items, which was the main purpose of the study. While GPS cluster investigations may be biased towards larger prey items (Bacon et al. 2011), I detected a considerable number of birds in the diet of lions. This detection of smaller prey suggests that my cluster parameters did not miss prey items the size of sooty grouse or larger. Of the 293 clusters that I investigated, I was unable to find prey remains at only ~9% of the sites, suggesting that the cluster parameters were not too conservative. Since I did not investigate less conservative cluster, I acknowledge that smaller prey items may make up a larger percentage of lions diet than I observed.

Coarse Scale Habitat Selection

For coarse scale habitat selection at kill sites at the study area level, there was support for 2 models that combined predictors from both the prey density and ambush

cover hypotheses. Both supported models included distance to water, slope, and western juniper basal area as predictors of kill sites. There was a negative relationship between distance to water and kill sites, indicating that kill sites occurred closer to water sources. This is important, as the study occurred on the tail end of an extreme drought (Mann and Gleick 2015), and during times of limited water prey utilize secondary and tertiary water sources, potentially making them more susceptible to predation (Thrash et al. 1995). However, I believe this effect to be small, as the confidence intervals overlapped 1 (Table 4). There was a positive relationship between kill site and slope, indicating that kill sites occurred on steeper slopes than random locations throughout the study area. Lions may utilize steeper slopes to their advantage when successfully killing their prey (Gladders 2003, Nichols 2017). There was also support for larger western juniper basal area at kill sites suggesting that larger trees provide lions with greater cover when stalking their prey. The second supported model included live conifer density as a predictor of kill site. I conclude that the effect of live conifer density is likely small, as confidence intervals overlapped 1 and the odds ratio was so close to 1. Overall, the models that combined predictors from both the prey density and the ambush cover hypotheses were ranked higher than models that kept them separate. Thus, I conclude that at the study area level, lions are killing their prey in areas where there are higher prey densities as well as increased ambush cover.

For the coarse scale selection of kill sites at the home range level, I identified 3 supported models (Table 5). The top model showed kill sites occurred in areas with larger

western juniper basal area than random points throughout lion's home ranges. Although the confidence intervals for western juniper basal area overlapped 1, they were skewed to the right, indicating some support for larger basal area. As discussed previously, lions may be utilizing these larger western junipers (or the vegetation associated with them) as sources of cover to from which to make their kills. The second ranked model included the variable conifer density, but there was little support for this with confidence intervals overlapping 1. The third ranked model included slope and distance to water. Kill sites occurred slightly closer to water and on slightly steeper slopes than random points, supported by findings of previous studies (Blake 2014, Nichols 2017), although the confidence intervals overlapped 1.

At the home range level, the top ranked models identifying kill sites did not contain predictor variables from both the prey density and ambush cover hypotheses, suggesting that scale may play a role in determining what lions are selecting for at kill sites. Compared to what is available throughout the study area, lions are likely killing prey where densities are high (Davidson et al. 2012). However, they would also need sufficient cover to kill their prey as shown by the top models being a combination of the prey density and ambush cover hypotheses. My model selection process was supported by a study that found that lions in three other regions of California establish their home ranges around high prey densities (Grigione et al. 2002). If prey is not limited throughout lions' home ranges, it is possible that they are killing prey in areas where ambush cover is sufficient (Davidson et al. 2012). Support for the first hypothesis indicates that lions in

Modoc establish their home ranges around pockets of western junipers with larger basal area. This suggests that western juniper basal area is likely more uniform throughout lions' home ranges than it is at the larger study area level, and that lions may not be making selections at this scale.

Fine Scale Habitat Selection

Other research has highlighted the importance of scale when analyzing habitat features of mountain lion kill sites, but only a few studies have analyzed habitat at a fine scale (Husseman 2003, Blake 2014). In this study, both of the top models for kill sites and points of first contact included the obstructed horizontal visibility variable. Specifically, horizontal visibility was lower at both kill sites and points of first contact, as was found in the Salmon River Mountains of Idaho and the Pryor Mountains of Montana and Wyoming (Husseman et al. 2003, Blake 2014). I predicted western junipers would strongly influence kill site selection due to the increase in western junipers on the Modoc Plateau (Young and Evans 1981, Bedell et al. 1993, Miller et al. 2005) and previous research finding that lions preferentially kill their prey in conifer stands (Logan and Irwin 1985, Husseman et al. 2003), juniper-pinyon stands (Laundré and Hernandez 2003), and juniper-mahogany stands (Blake 2014). Contrary to what I predicted, distance to western juniper did not arise as an important factor in habitat selection at kill sites and points of first contact. At a fine scale it seems that lions were not specifically seeking out western junipers as sources of cover; rather they were using whatever cover was available to them

on the landscape to obscure their profile from the prey items. This is further supported by the absence of conifer presence as a variable in the top supported models for predicting kill sites and points of first contacts. These results suggest that it is not the type of cover that is important, but rather that there is sufficient cover for stalking.

The lack of a regular fire cycle in the study area has allowed for more than just the succession of western junipers; rather it has affected all vegetation on the landscape, such as the increase in both woody and herbaceous vegetation (Miller and Wigand 1994). This increase in vegetation as a whole makes more cover available on the landscape for lions to use. Especially since lions may not need to be fully concealed, rather they may only require sufficient cover to break up their profile from the prey's perspective, as when stalking mule deer using only a fence line for cover (Logan and Irwin 1985).

It has been suggested that when hunting, lions utilize both topography as well as vegetative cover (Logan and Irwin 1985). Slope was found to be an important predictor of lion kill sites in the Sierra National Forest of California (Nichols 2017) and at lion feeding sites on Vancouver Island, British Columbia (Gladders 2003). However, the fine scale analyses did not include slope as a predictor in the top models for kill sites nor points of first contact. This could be due to the relatively uniform slopes available to lions on the Modoc Plateau. Because slope was not included in the top fine scale models, it is possible that the ample vegetative cover in my study area allows lions to kill without utilizing slope at this level. In a similar habitat type of juniper and mountain mahogany in

the Pryor Mountains, slope was similarly excluded from top models for fine scale kill site selection (Blake 2014).

Several other studies have included the proximity of water sources as a predictor of felid kill sites, but found that at a fine scale, big cats were selecting for cover rather than proximity to water (Hopcraft et al. 2005, Balme et al. 2007, Davidson et al. 2012). This trend of distance to water being less important than cover at fine scale habitat selection at kill sites may be related to the distribution of water and prey on the landscape. It is common for the distribution of water on the Modoc Plateau to vary seasonally, and if I included seasonality in my analyses, then water may have been a more important predictor of kill sites and points of first contact (Blake and Gese 2016). It is also possible that lions establish their home ranges around areas with sufficient water to support abundant prey, and they utilize cover within the areas where prey already exist, indicating that the scale of this habitat variable is important for selection.

Habitat Variation across Kill Sites by Species

I observed different habitat characteristics at kill sites of different prey species. Mule deer were killed on steeper slopes than were feral horses. This may be explained by the terrain that these species prefer, with mule deer using steeper slopes than horses (Ganskopp 1983). It is also possible that steeper slopes were more available to deer, which were ubiquitous throughout the study area. Compared to deer, horses were confined within the flatter, more open Devil's Garden Horse Management Unit.

I also observed lions killing pronghorn in areas with larger western juniper basal area than the sites where they killed mule deer. This contradicted what I expected, as pronghorn typically prefer open habitats (Kitchen 1974, Miller et al. 2005) and mule deer are more capable of utilizing forested and edge habitats (Kufeld et al 1988, Kie et al. 2002). This suggests that lions require junipers with larger basal area to provide more cover when killing pronghorn, perhaps because pronghorn have excellent eyesight (Lubinski and Herren 2000). This is supported by pronghorn evolving in open habitats, utilizing their vision to detect sources of cover on the landscape (Kitchen 1974, Bromley 1977). However, while pronghorn have excellent vision at a distance, they lack visual acuity at close distances (Kitchen 1974), and therefore any cover capable of concealing ambush predators may make them vulnerable. Pronghorn also rely heavily on vision for social cues from conspecifics within their herd for predator avoidance (Bromley 1977), thus it is possible that western junipers of larger basal area provide more impediments to these predator avoidance strategies.

Although there were differences in the mean live conifer density and mean distance to water between kill sites across species, these were not significant. This was in part due to the large variation in values across the kill sites for all of the species observed. This is likely a product of the mosaic of habitats found in the study area. Although there was the largest difference in live conifer density means between feral horses and coyotes, I still observed occasions where lions killed coyotes in areas with low live conifer density. Because coyotes are generalists and have the ability to thrive in high and low

forest cover (Quinn 1997, Boisjoly et al. 2010), my findings of lions killing coyotes across a wide spread of values for live conifer density do not seem anomalous. Similarly, I did not detect significant differences for distance to water across individual species kill sites. Water availability has been shown to dictate space use of mule deer (Jenkins and Wright 1988, Boroski and Mossman 1996), feral horses (Miller 1983), pronghorn (Kitchen 1974, Yoakum 1979), and coyotes (Atwood et al. 2011). However, if water is limited across the Modoc Plateau, these four species may be utilizing water sources similarly.

Management Implications

The larger western juniper found in core areas of lions' home ranges indicates their importance to mountain lions in this region. If lions are spending nearly half of their time in areas of larger western juniper basal area, they may be impacted by the large-scale western juniper cuts planned by the U.S. Forest Service (USFS) and Bureau of Land Management (BLM). As a result of the juniper removal effort, there is potential for mountain lion home ranges to shift and expand to incorporate new areas with sufficient cover. The impact of large territorial animals increasing the size of their home ranges may mean that the study area will support a lower density of lions, or that lions may expand their ranges outside of the study area. I recommend that lions continue to be monitored after juniper removal to see if there are abrupt shifts in home range size or fidelity. In coordination with the USFS and BLM, there is potential to assess the space

utilization by lions before and after large scale cuts are conducted. Interestingly, several lions within the study area killed prey in close proximity to western junipers that recently had been cut down, but left on the landscape. It is possible that lions have the ability to use these downed junipers for cover as well, so using prescribed burns to accompany juniper removals may be a more impactful way to reduce the zones of risk for ungulates within the study area. Prescribed burns will also help reduce cover in forms other than western junipers, which I found to be important to lions at the fine scale.

Based on the rough population estimates of ungulates on the landscape from CDFW (California Department of Fish and Wildlife 2018, 2019), IWS (unpublished data) and the USFS (Modoc National Forest 2019), the composition of ungulates in the diet of lions seems to track the relative abundance of what is available to them (Kunkel et al. 1999, Kortello et al. 2007, Valeix et al. 2012). Lions of the Modoc Plateau are likely not selecting any particular prey type, rather following the trends of what prey is abundant within their respective home ranges (Iriarte et al. 1990, Karanth and Sunquist 1995, Davidson et al. 2013). I did not find pronghorn to represent a large proportion of any of the lion's diets, but if pronghorn populations increase, there is potential for more lion predation to ensue.

Although male lion M166 appeared to be a feral horse specialist, a single lion is not capable of keeping the regional feral horse population in check (Greger and Romney 1999, Turner and Morrison 2001, Knopff et al. 2010). To further understand the impact of lions on the feral horse population, I recommend capturing and collaring more lions in

the feral horse management units to see if there are other feral horse specialists. As the Devil's Garden unit is scheduled to remove 1,000 feral horses annually for the next 3 years, it may be beneficial to monitor diets of lions in this area as prey densities shift.

Another benefit to understanding the prey composition of these collared mountain lions is that it can provide managers with baseline data for the diet of lions prior to wolf colonization of the study area. With established wolf packs to the north, south and west of the study area, it may only be a matter of time before they establish in Modoc County. Wolves have the potential to impact lions directly, through mortality and carcass displacement (White and Boyd 1989, Kortello et al. 2007), or indirectly by altering lion prey selection and spatial movement patterns (Alexander et al. 2006, Kortello et al. 2007). I now have data on prey composition, home range metrics, and habitat selection for lions at the study area, home range, and within-home range levels. If wolves establish within the study area, managers can monitor behavioral changes in lions in both their foraging habits and habitat selection. Modoc County is unique in that it offers a significant source of secondary prey: feral horses. Unlike previous interaction studies in Yellowstone (Bartnick et al. 2013) and Banff National Parks (Kortello et al. 2007), in Modoc, feral horses are available as secondary prey items to alleviate the immediate impacts of wolf colonization on lions, as there is large dietary overlap between these two predators in a multi-prey system (Kunkel et al. 1999). A study in Banff National Park showed that once elk densities were low, wolves switched to consuming deer, which then pressured lions to predate more upon bighorn sheep (Kortello et al. 2007). In Modoc, elk

densities are already low, and the primary ungulate prey available on the landscape is mule deer (California Department of Fish and Wildlife 2018, 2019). With the potential for prey switching and a change in diet composition of lions on the Modoc Plateau, it would be prudent to continue monitoring the foraging habits of lions as wolves make their way into the study area.

The feral horse population in Modoc is growing rampantly, and wildlife managers may wish to reduce this population in an effort to improve habitat for native wildlife (Crane et al. 1997, Beever and Brussard 2000, Beever et al. 2008). If additional mountain lions (other than M166) are specializing in feral horses, there is potential for foal recruitment to be limited through predation by lions (Turner and Morrison 2001). Wildlife managers have the ability to improve lion hunting habitat within the horse management areas by increasing the amount of cover available to lions in areas that have flatter slopes.

Conversely, mule deer populations are declining across the Modoc Plateau (Clements and Young 1997, California Department of Fish and Wildlife 2019). The most effective way to reduce predation by lions is through the alteration of habitat, reducing areas of high risk for prey (Blake and Gese 2016). Habitat characteristics were broadly similar across species. This suggests that lions utilize roughly the same habitat to kill multiple prey types. Based on this study's resource selection functions, the most important factor at a fine scale is the obstructed horizontal visibility. At a coarser scale, lions killed their prey closer to water, on steeper slopes, in lower conifer densities and in

areas with larger western juniper basal area. If drought persists in the study area, it may be beneficial for managers to construct supplemental water sources. I recommend these water sources be placed in areas that have relatively flat slope, low conifer densities, and small western juniper basal area, yet also have high visibility for the prey utilizing them.

LITERATURE CITED

- Ackerman, B. B., F. G. Lindzey, and T. P. Hemker. 1984. Cougar food habits in southern Utah. *The Journal of Wildlife Management* 48:147–155.
- Alexander, S. M., T. B. Logan, and P. C. Paquet. 2006. Spatio-temporal co-occurrence of cougars (*Felis concolor*), wolves (*Canis lupus*) and their prey during winter: a comparison of two analytical methods. *Journal of Biogeography* 33:2001–2012.
- Allen, M. L., L. M. Elbroch, D. S. Casady, and H. U. Wittmer. 2014. Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. *Canadian Journal of Zoology* 92:397–403.
- Altendorf, K. B., and J. W. Laundre. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy* 82(2):430–439.
- American Association of Equine Practitioners. 1966. Official Guide for Determining the Age of the Horse. Fort Dodge Laboratories.
<https://books.google.com/books?id=Ew_TxgEACAAJ>.
- Anderson, C. R., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. *The Journal of Wildlife Management* 67(2):307–316.
- Anderson, M. K. 2018. The use of fire by Native Americans in California. Pages 381–398 in J.W. Van Wagtendonk, editor. *Fire in California's ecosystems*. University of California Press, Alameda, USA.
- Atwood, T. C., T. L. Fry, and B. R. Leland. 2011. Partitioning of anthropogenic water sites by desert carnivores. *The Journal of Wildlife Management* 75(7): 1609-1615.
- Bacon, M. M., G. M. Becic, M. T. Epp, and M. S. Boyce. 2011. Do GPS clusters really work? Carnivore diet from scat analysis and GPS telemetry methods. *Wildlife Society Bulletin* 35:409–415.
- Balme, G., L. Hunter, and R. Slotow. 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* 74:589–598.
- Bartnick, T. D., T. R. Van Deelen, H. B. Quigley, and D. Craighead. 2013a. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. *Canadian Journal of Zoology* 91:82–93.

- Bauer, J. W., K. A. Logan, L. L. Sweanor, and W. M. Boyce. 2005. Scavenging behavior in puma. C. A. Jones, editor. *The Southwestern Naturalist* 50:466–471.
- Bedell, T. E., L. E. Eddleman, T. Deboodt, C. Jacks. 1993. Western Juniper-Its impact and management in Oregon rangelands. Oregon State University Extension Service, Corvallis, Oregon, USA.
- Beever, E. A., and P. F. Brussard. 2000. Examining ecological consequences of feral horse grazing using exclosures. *Western North American Naturalist* 60(3):236-254.
- Beever, E. A., R. J. Tausch, and W. E. Thogmartin. 2008. Multi-scale responses of vegetation to removal of horse grazing from Great Basin (USA) mountain ranges. *Plant Ecology* 196:163–184.
- Beier, P., D. Choate, and R. H. Barrett. 1995. Movement patterns of lions during different behaviors. *Journal of Mammalogy* 76:1056–1070.
- Belden, R. C., Frankenberger W. B., McBride R. T., Schwikert S. T. 1988. Panther habitat use in southern Florida. *The Journal of Wildlife Management* 52(4):660–663.
- Blake, L. W. 2014. Foraging ecology of cougars in the Pryor Mountains of Wyoming and Montana. Thesis, Utah State University, Logan, USA.
- Blake, L. W., and E. M. Gese. 2016. Resource selection by cougars: Influence of behavioral state and season: cougar resource selection. *The Journal of Wildlife Management* 80:1205–1217.
- Boisjoly, D., J.-P. Ouellet, and R. Courtois. 2010. Coyote Habitat Selection and Management Implications for the Gaspésie Caribou. *Journal of Wildlife Management* 74:3–11.
- Boroski, B. B., and A. R. Mossman. 1996. Distribution of mule deer in relation to water sources in northern California. *Journal of Wildlife Management* 60:770–776.
- Bromley, P.T. 1977. Aspects of the behavioural ecology and sociobiology of the pronghorn (*Antilocapra americana*). Thesis, University of Calgary, Calgary, CA.
- Brown D. E., D. Warnecke, T. McKinney. 2006. Effects of midsummer drought on mortality of doe pronghorn (*Antilocapra americana*). *The Southwestern Naturalist*. 51(2):220–225.

- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- California Department of Fish and Wildlife [CDFW]. 2018. Wildlife Branch- Game Management. Elk conservation and management plan.
<<http://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=162912&inline>>
- California Department of Fish and Wildlife [CDFW]. 2019. Wildlife Branch- Game Management. California's deer population estimates.
<<https://www.wildlife.ca.gov/Conservation/Mammals/Deer/Population#32712445-population-by-hunt-zone>>
- Carpenter, L. H. 1998. Deer in the West. In Proceedings of the 1997 Deer/Elk Workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.
- Clements, C. D., and J. A. Young. 1997. A Viewpoint: Rangeland Health and Mule Deer Habitat. *Journal of Range Management* 50:129-138.
- Coppedge, B. R., D. M. Engle, S. D. Fuhlendorf, R. E. Masters, and M. S. Gregory. 2001. Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA. *Landscape Ecology* 16:677–690.
- Crane, K. K., M. A. Smith, and D. Reynolds. 1997. Habitat selection patterns of feral horses in southcentral Wyoming. *Journal of Range Management* 50:374-380.
- Cunningham, S. C., C. R. Gustavson, and W. B. Ballard. 1999. Diet selection of mountain lions in southeastern Arizona. *Journal of Range Management* 52:202-207.
- Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, M. A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144(11):2573–2584.
- Davidson, Z., M. Valeix, A. J. Loveridge, J. E. Hunt, P. J. Johnson, H. Madzikanda and D. W. Macdonald. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy* 93(3):677–685.
- Davidson, Z., M. Valeix, F. Van Kesteren, A. J. Loveridge, J. E. Hunt, F. Murindagomo, D. W. Macdonald. 2013. Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. *PLOS One* 8(2):1–10.

- D'Eon, R. G., and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. *Journal of Mammalogy* 86:736–744.
- Dickson, B. G., and P. Beier. 2002. Home-range and habitat selection by adult cougars in southern California. *The Journal of Wildlife Management* 66:1235-1245.
- Elbroch, L. M., B. D. Jansen, M. M. Grigione, R. J. Sarno, and H. U. Wittmer. 2013. Trailing hounds vs foot snares: comparing injuries to pumas *Puma concolor* captured in Chilean Patagonia. *Wildlife Biology* 19:210–216.
- Elbroch, L. M., and H. U. Wittmer. 2013. The effects of puma prey selection and specialization on less abundant prey in Patagonia. *Journal of Mammalogy* 94:259–268.
- Elbroch L. M., M. L. Allen, B. H. Lowery, H. U. Wittmer. 2014. The difference between killing and eating: ecological shortcomings of puma energetic models. *Ecosphere*. 5(5):1-16.
- Engstrom, M. D. and Maxwell, T. C., 1988. Records of lion (*Felis concolor*) from the western Edwards Plateau of Texas. *Texas Journal of Science* 40(4):450-452.
- Funston, P. J., and M. G. L. Mills. 2006. The influence of lion predation on the population dynamics of common large ungulates in the Kruger National Park. *South African Journal of Wildlife Research* 36:9-22.
- Ganskopp, D. C. 1983. Habitat use and spatial interactions of cattle, wild horses, mule deer and California bighorn sheep in the Owyhee Breaks of southeast Oregon. Thesis, Oregon State University, Corvallis, USA.
- Ganskopp, D., and M. Vavra. 1987. Slope use by cattle, feral horses, deer, and bighorn sheep. *Northwest Science* 61(2):74-81.
- Gladders, A. D. 2003. Predation behavior of Vancouver Island cougar (*Puma concolor vancouverensis*) and its relation to micro- and macroscale habitat. Thesis, University of British Columbia, Vancouver, Canada.
- Goldsmith, A. E. 1990. Vigilance behavior of pronghorns in different habitats. *Journal of Mammalogy* 71:460–462.
- Greger P. D., E. M. Romney. 1999. High foal mortality limits growth of a desert feral horse population in Nevada. *The Great Basin Naturalist* 59(4):374-379.

- Grigione, M. M., P. Beier, R. A. Hopkins, D. Neal, W. D. Padley, C. M. Schonewald, & M. L. Johnson. 2002. Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). *Animal Conservation* 5(4):317–324.
- Harveson, L. A., M. E. Tewes, N. J. Silvy, and J. Rutledge. 2000. Prey use by mountain lions in southern Texas. *The Southwestern Naturalist* 45:472–476.
- Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. MacDonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home range analyses with least-squares cross-validation. *Journal of Animal Ecology* 74:455–463.
- Hernández, L., and J. W. Laundré. 2005. Foraging in the ‘landscape of fear’ and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology* 11(3):215–220.
- Holmes, B. R., and J. W. Laundré. 2006. Use of open, edge and forest areas by pumas *Puma concolor* in winter: are pumas foraging optimally? *Wildlife Biology* 12:201–209.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12(2):197–229.
- Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance: Prey accessibility in Serengeti lions. *Journal of Animal Ecology* 74:559–566.
- Horn, H. S. 1966. Measurement of “overlap” in comparative ecological studies. *The American Naturalist* 100(914):419–424.
- Hornocker, M. G. 1970. An analysis of lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs* 20:3–39.
- Hubbard, R. E., & R. Hansen. 1976. Diets of wild horses, cattle, and mule deer in the Piceance Basin, Colorado. *Journal of Range Management*, 29(5):389–392.
- Husseman, J. S., D. L. Murray, G. Power, C. Mack, C. R. Wenger, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* 101(3):591–601.

- Iriarte, J. A., W. L. Franklin, W. E. Johnson, and K. H. Redford. 1990. Biogeographic variation of food habits and body size of the America puma. *Oecologia* 85:185–190.
- Jenkins K. J., R. G. Wright. 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. *Journal of Applied Ecology* 25(1):11–24.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Karanth, K. U. and M. E. Sunquist. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology* 64(4): 439–450.
- Keller B. J., J. J. Millspaugh., C. Lehman, G. Brundige, T. W. Mong. 2013. Adult pronghorn (*Antilocapra americana*) survival and cause-specific mortality in Custer State Park, SD. *The American Midland Naturalist*. 170(2):311–322.
- Kertson, B. N., R. D. Spencer, and C. E. Grue. 2011. Cougar prey use in a wildland–urban environment in western Washington. *Northwestern Naturalist* 92:175–185.
- Kie, J. G., T. Bowyer, M. C. Nicholson, B. B. Boroski and E. R. Loft. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology* 83(2):530-544.
- Kitchen, D. W. 1974. Social Behaviour and Ecology of the pronghorn. *Wildlife Monographs* 38:3-96.
- Knopff K. H., A. A. Knopff, A. Kortello, M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. *Journal of Wildlife Management* 74(7):1435-1447.
- Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among lions, bobcats, and coyotes. *Journal of Mammalogy* 72:391–396.
- Kortello, A., T. Hurd, and D. Murray, 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. *Écoscience*, 14(2):214–222.
- Kufeld, R. C., D. C. Bowden, and D. L. Schrupp. 1988. Influence of hunting on movements of female mule deer. *Journal of Range Management* 41:70-72.

- Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park Montana. *The Journal of Wildlife Management* 63:901-910.
- Laing, S. P. 1988. Cougar habitat selection and spatial use patterns in southern Utah. - Thesis, University of Wyoming, Laramie, USA.
- Laundré, J. W., and L. Hernández. 2003. Winter hunting habitat of pumas *Puma concolor* in northwestern Utah and southern Idaho, USA. *Wildlife Biology* 9:123–129.
- Leopold, B. D., and P. R. Krausman. 1986. Diets of 3 predators in Big Bend National Park, Texas. *The Journal of Wildlife Management* 50:290-295.
- Loft, E. R., J. W. Menke, and J. G. Kie. 1991. Habitat shifts by mule deer: the influence of cattle grazing. *The Journal of Wildlife Management* 55:16-26.
- Logan K. A., Irwin L. L. 1985. Lion habitats in the big horn mountains, Wyoming. *Wildlife Society Bulletin*, 13:257–262.
- Logan, K. A., L. L. Sweanor, T. K. Ruth, and M. G. Hornocker. 1996. Cougars of the San Andrés Mountains, New Mexico. Final Report Project W-128-R for New Mexico Department of Game and Fish, Santa Fe, USA.
- Logan, K. A. and Sweanor, L. L., 2001. Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore. Island Press.
- Lowrey B., Elbroch L. M., and L. Broberg L. 2016. Is individual prey selection driven by chance or choice? A case study in cougars (*Puma concolor*). *Mammal Research*. 61(4):353–359.
- Lubinski, P. M., and V. Herren. 2000. An introduction to pronghorn biology, ethnography and archaeology. *Plains Anthropologist* 45:3–11.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. Erikson. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic.
- Mann, M. E., and P. H. Gleick. 2015. Climate change and California drought in the 21st century. *Proceedings of the National Academy of Sciences* 112:3858–3859.
- Mech, L. D. 1967. Telemetry as a Technique in the Study of Predation. *The Journal of Wildlife Management* 31:492-496.

- Miller, R. 1983. Habitat use of feral horses and cattle in Wyoming's Red Desert. *Journal of Range Management* 36:195-198.
- Miller, R. F., and P. E. Wigand. 1994. Holocene Changes in Semiarid Pinyon-Juniper Woodlands. *BioScience* 44:465–474.
- Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. *Journal of Range Management* 52:550-559.
- Miller, R. F., J. D. Bates, T. J. Svejcar, F. B. Pierson, and L. E. Eddleman. 2005. Biology, ecology, and management of western juniper. Oregon State University Agricultural Experiment Station Technical Bulletin 152, Corvallis, Oregon, USA.
- Modoc National Forest. 2019. Modoc National Forest, U.S. Forest Service. Devil's garden horses: data collection.
<<https://www.fs.usda.gov/detail/modoc/landmanagement/resourcemanagement/?cid=fseprd594041>>
- Morrison, C. D., M. S. Boyce, S. E. Nielsen, and M. M. Bacon. 2014. Habitat selection of a re-colonized cougar population in response to seasonal fluctuations of human activity: Cougar Habitat Use in Response to Human Activity. *The Journal of Wildlife Management* 78:1394–1403.
- Murphy, M. K., G. Felzien, M. Hornocker, and T. Ruth. 1998. Encounter competition between bears and cougars: some ecological implications. *Ursus* 10:55–60.
- Musgrave, M. E. 1926. Some habits of lions in Arizona. *Journal of Mammalogy* 7:282-285.
- Nellis, C. H., S. P. Wetmore, and L. B. Keith. 1978. Age-related characteristics of coyote canines. *The Journal of Wildlife Management* 42:680–683.
- Nichols, B. C. Foraging ecology of mountain lions in the Sierra National Forest, California. Thesis, Utah State University, Logan, USA.
- O'Brien, R. M. 2007. A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity* 41:673–690.
- Ockenfels R. A., Alexander A., Ticer C. D., Carrel W. K. 1994. Home ranges, movement patterns, and habitat selection of pronghorn in central Arizona. Arizona Game and Fish Department Technical Report.13–80.

- Ordway, L. L., and P. R. Krausman. 1986. Habitat use by desert mule deer. *The Journal of Wildlife Management* 50:677-683.
- Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. *The American Naturalist* 153:492–508.
- Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. *Journal of Mammalogy* 80:986–992.
- Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes: Effects of hunting style, body size, and reproductive status. *Journal of Mammalogy* 81(2):462-472.
- Pierce, B. M., and V. C. Bleich. 2003. Mountain Lion (*Puma concolor*). *Wild Mammals of North America* 2:744–757.
- Pierce II, R. A., J. A. Sumners, and E. B. Flinn. 2011. Aging a deer by examining its jawbone. University of Missouri Extension.
- Pierson, F. B., C. J. Williams, P. R. Kormos, S. P. Hardegree, P. E. Clark, and B. M. Rau. 2010. Hydrologic vulnerability of sagebrush steppe following pinyon and juniper encroachment. *Rangeland Ecology & Management* 63:614–629.
- Quinn, T. 1997. Coyote (*Canis latrans*) habitat selection in urban areas of western Washington via analysis of routine movements. *Northwest Science* 71(4):289-297.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Rickard, W. H. 1985. Experimental cattle grazing in a relatively undisturbed shrubsteppe community. *Northwest Science* 59:66–72.
- Riegel G. M., R.F. Miller, C.N. Skinner, S.E. Smith. 2006. Northeastern plateaus bioregion. N.G. Sugihara, J. van Wagendonk, K.E. Shaffer, J. Fites-Kaufman, A.E. Thode (Eds.), *Fire in California's Ecosystems*, California: University of California Press, Berkeley 225–263.
- Robinette, W. L., J. S. Gashwiler, and O. W. Morris. 1959. Food habits of the cougar in Utah and Nevada. *Journal of Wildlife Management* 23:261-273.

- Rominger, E. M., H. A. Whitlaw, D. L. Weybright, W. C. Dunn, and W. B. Ballard. 2004. The influence of lion predation on bighorn sheep translocations. *Journal of Wildlife Management* 68:993–999.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396–403.
- Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, A. A. Abraham. 2007. Habitat selection of Rocky Mountain Elk in a nonforested environment. *Journal of Wildlife Management* 71(3):868-874.
- Seaman D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63(2):739–747.
- Seidensticker J. C., M. G. Hornocker, W. V. Wiles, J. P. Messick. 1973. Lion social organization in the Idaho Primitive Area. *Wildlife Monographs*. (35):3–60.
- Sollmann, R., M., M. Furtado, H. Hofer, A. T. Jacomo, N. M. Tôrres, and L. Silveira. 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology-Zeitschrift für Säugetierkunde* 77:41–46.
- Sweitzer, R.A., S. H. Jenkins, and J. Berger. 1997. Near-extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin Desert. *Conservation Biology* 11:1407–1417.
- Thompson, D. J., D. M. Fecske, J. A. Jenks, and A. R. Jarding. 2009. Food habits of recolonizing cougars in the Dakotas: prey obtained from prairie and agricultural habitats. *The American Midland Naturalist* 161:69–75.
- Thrash, I., G. K. Theron, and J.D.P. Bothma. 1995. Dry season herbivore densities around drinking troughs in the Kruger National Park. *Journal of Arid Environments* 29:213–219.
- Turner Jr. J. W., and Morrison M. L. 2001. Influence of predation by lions on numbers and survivorship of a feral horse population. *The Southwestern Naturalist* 2:183–190.

- Valeix M., G. Hemson, A. J. Loveridge, G. Mills, and D. M. Macdonald. 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology* 49:73–81.
- Villepique, J. T., B. M. Pierce, V. C. Bleich, and R. T. Bowyer. 2011. Diet of cougars (*Puma concolor*) following a decline in a population of mule deer (*Odocoileus hemionus*): Lack of evidence for switching prey. *The Southwestern Naturalist* 56:187–192.
- White, P. A., and D. K. Boyd. 1989. A cougar, *Felis concolor*, kitten killed and eaten by gray wolves, *Canis lupus*, in Glacier National Park, Montana. *Canadian field-naturalist*. Ottawa ON, 103(3):408–409.
- Yoakum J. D. 1972. Antelope-vegetative relationships. *Antelope States Workshop Proceedings* 5:171-177.
- Yoakum J. D. 1979. Managing rangelands for pronghorns. *Rangelands* 1(4):146–148.
- Young, J. A., and R. A. Evans. 1981. Demography and fire history of a western juniper stand. *Journal of Range Management* 34:501-505.
- Zou, C. B., D. J. Turton, R. E. Will, D. M. Engle, and S. D. Fuhlendorf. 2014. Alteration of hydrological processes and streamflow with juniper (*Juniperus virginiana*) encroachment in a mesic grassland catchment: alteration of hydrological processes after juniper encroachment. *Hydrological Processes* 28:6173–6182.

APPENDIX A

Appendix A: A Linear Discriminant Function for Habitat Characteristics at Kill Sites

I trained a discriminant function analysis using a random subset of 60% of the kill site data, and reserved the remaining 40% for testing. The proportion of trace for separation was 69.19% for LD1, 29.45% for LD2, and 1.36% for LD3. With the training data, the linear discriminants accurately predicted the species of 71.19% of the kill sites. Using the testing data, the linear discriminant functions accurately predicted the species for 61.54% of the kill sites.

Table A1. The species predicted by the discriminant function based on the subset of training data. The predicted values are depicted by the rows and the actual species are represented by the columns. For the training data, the linear discriminant functions accurately predicted 71.2% of the species.

		Actual			
		<i>Mule Deer</i>	<i>Feral horse</i>	<i>Pronghorn</i>	<i>Coyote</i>
Predicted	<i>Mule Deer</i>	41	11	2	1
	<i>Feral horse</i>	0	0	0	0
	<i>Pronghorn</i>	1	0	0	0
	<i>Coyote</i>	1	0	1	1

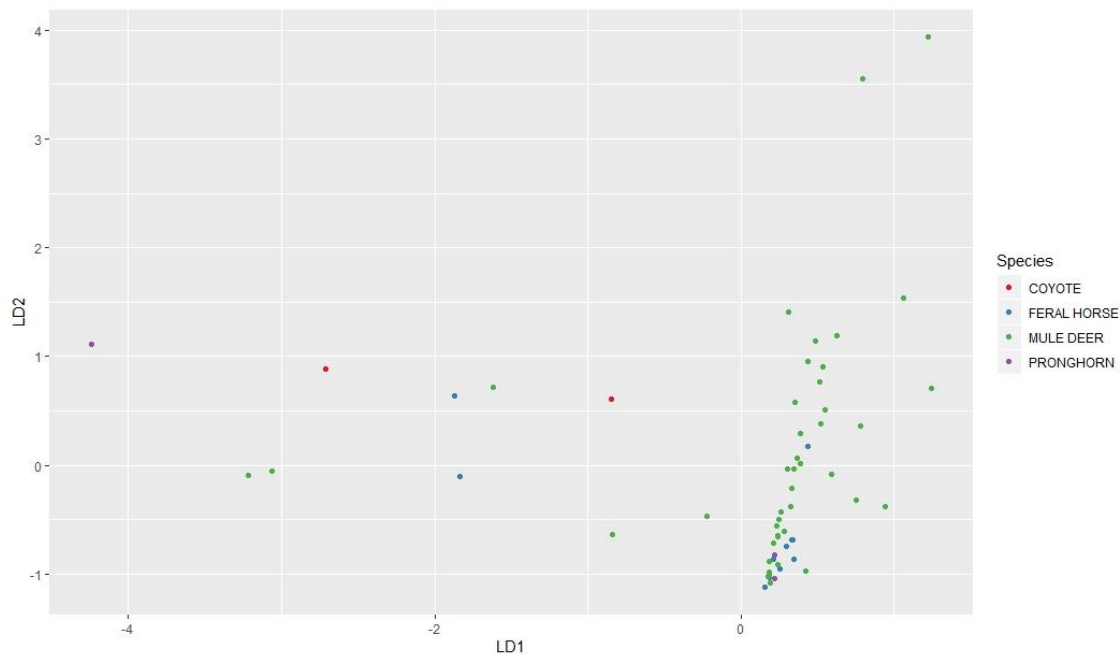


Figure A1. A linear discriminant function which depicts how LD1 and LD2 are separating differences in kill site characteristics of 4 species preyed on by mountain lions in Modoc and Lassen counties, CA between 2016– 2018.

Table A2. The species predicted by the discriminant function based on the subset of testing data. The predicted values are depicted by the rows and the actual species are represented by the columns. For the testing data, the linear discriminant functions accurately predicted 61.5% of the species.

		Actual			
		<i>Mule Deer</i>	<i>Feral horse</i>	<i>Pronghorn</i>	<i>Coyote</i>
Predicted	<i>Mule Deer</i>	24	7	5	3
	<i>Feral horse</i>	0	0	0	0
	<i>Pronghorn</i>	0	0	0	0
	<i>Coyote</i>	0	0	0	0

APPENDIX B

Appendix B: Home Ranges and Western Juniper Basal Area

The figures below show the home ranges for GPS collared mountain lions within Modoc and Lassen counties, CA. The home ranges were created using 95, 85, and 50% kernel density estimates in program *adehabitat* in R studio. The home ranges are overlaid on a LEMMA western juniper basal area layer, with darker red indicating western juniper of larger basal area per hectare.

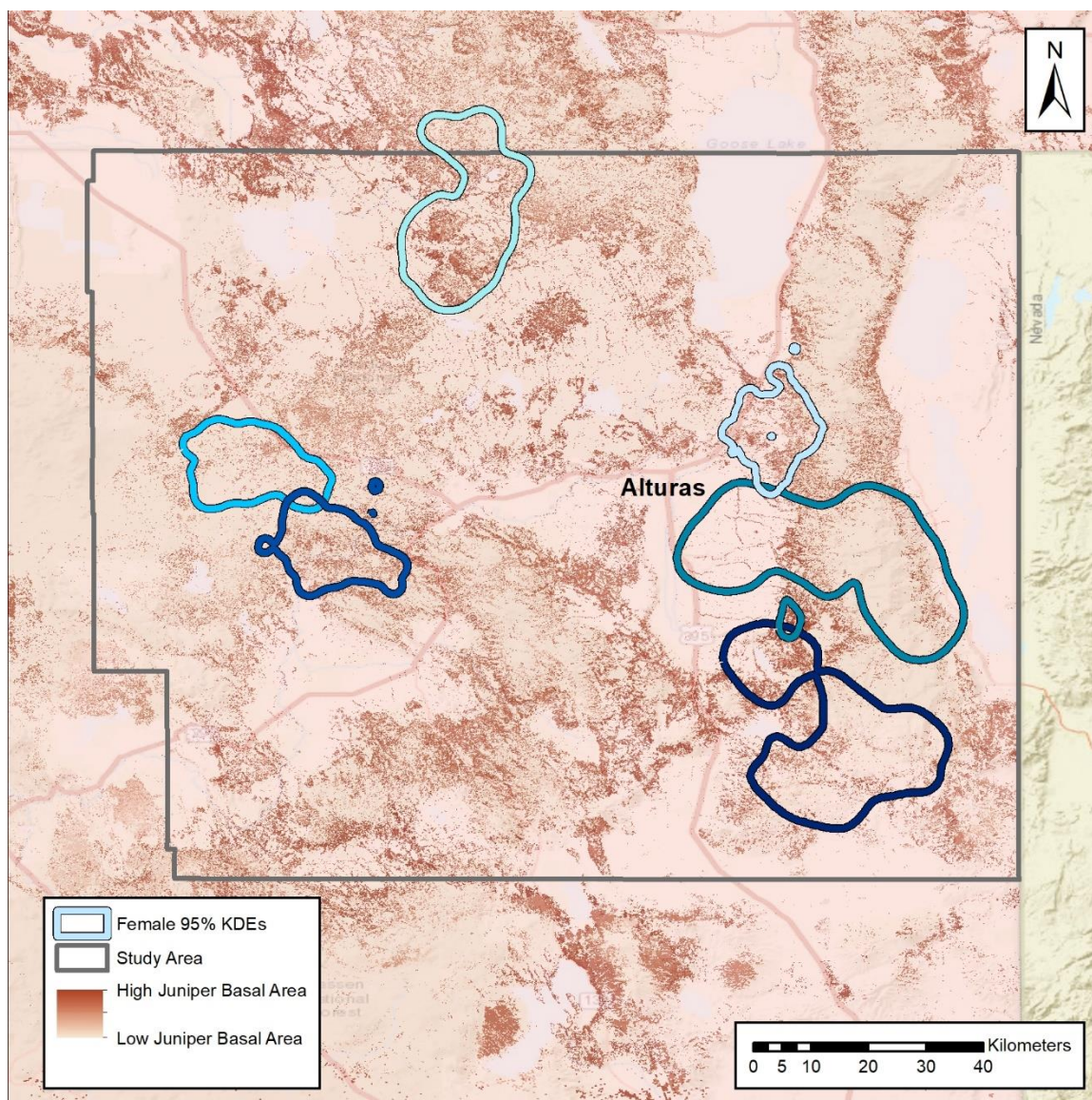


Figure B1. Female 95% kernel density estimates for GPS collared mountain lions in Modoc and Lassen counties, CA. Larger western juniper basal area is indicated by darker shades of red.

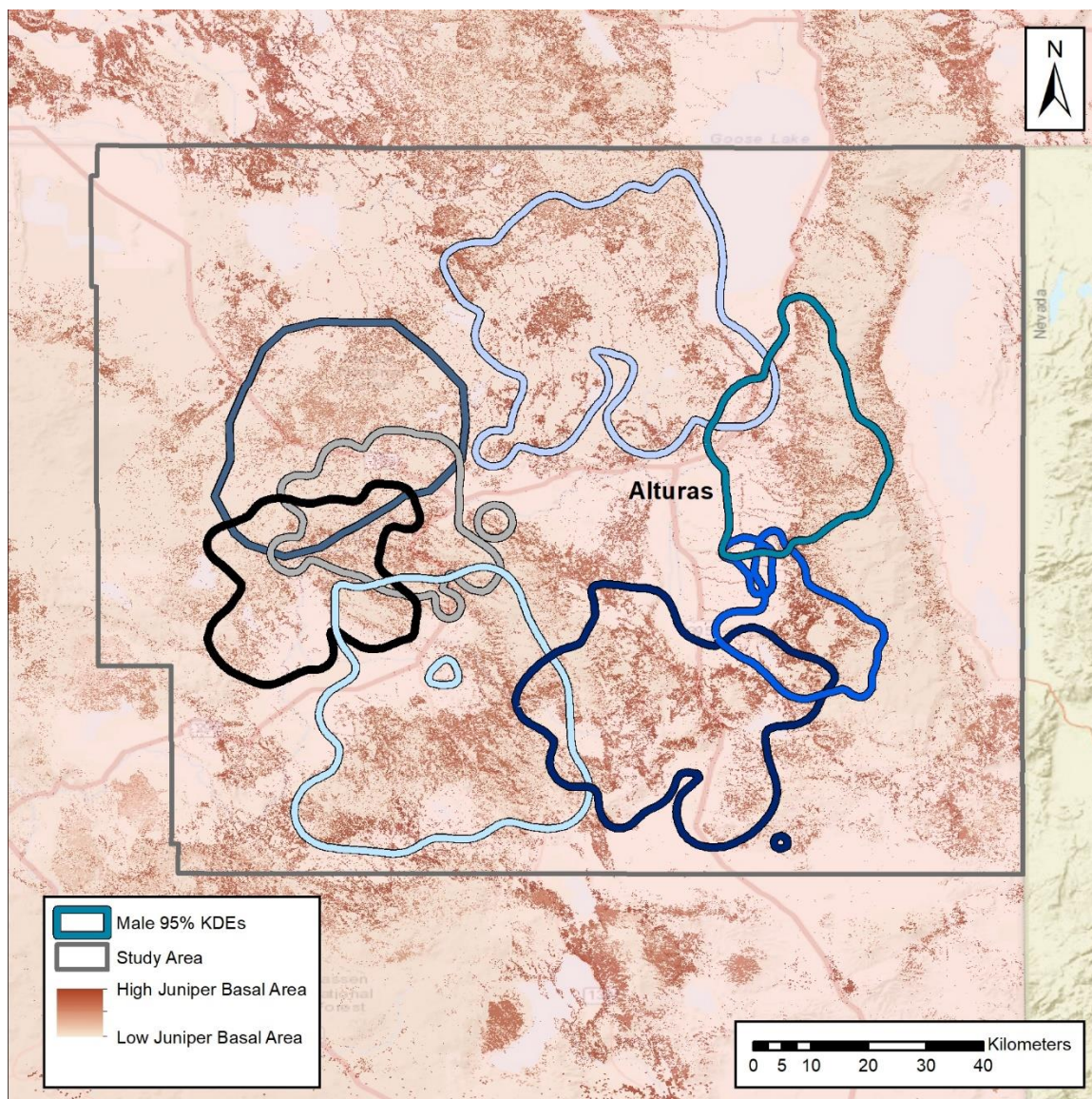


Figure B2. Male 95% kernel density estimates for GPS collared mountain lions in Modoc and Lassen counties, CA. Larger western juniper basal area is indicated by darker shades of red.

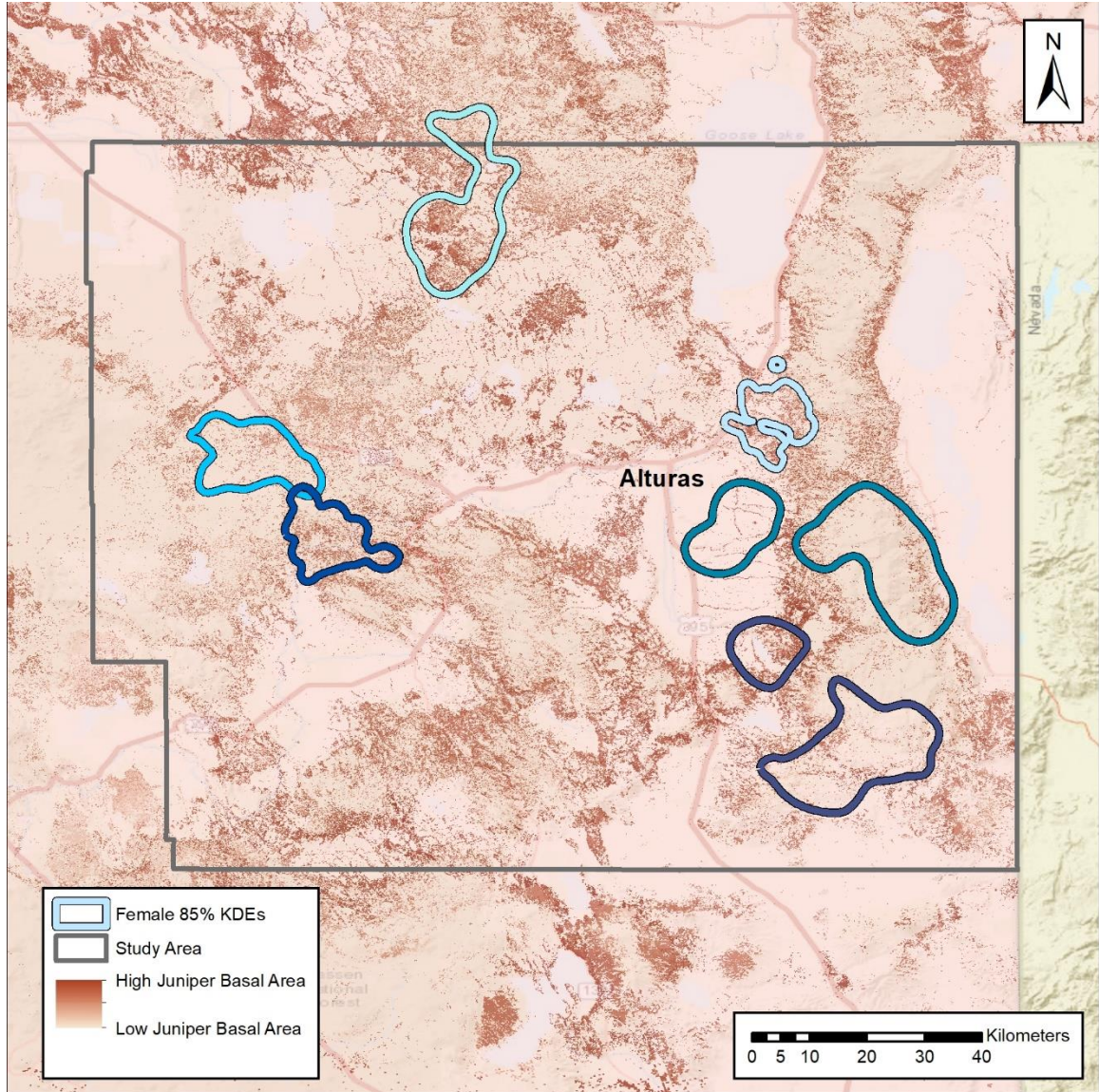


Figure B3. Female 85% kernel density estimates for GPS collared mountain lions in Modoc and Lassen counties, CA. Larger western juniper basal area is indicated by darker shades of red.

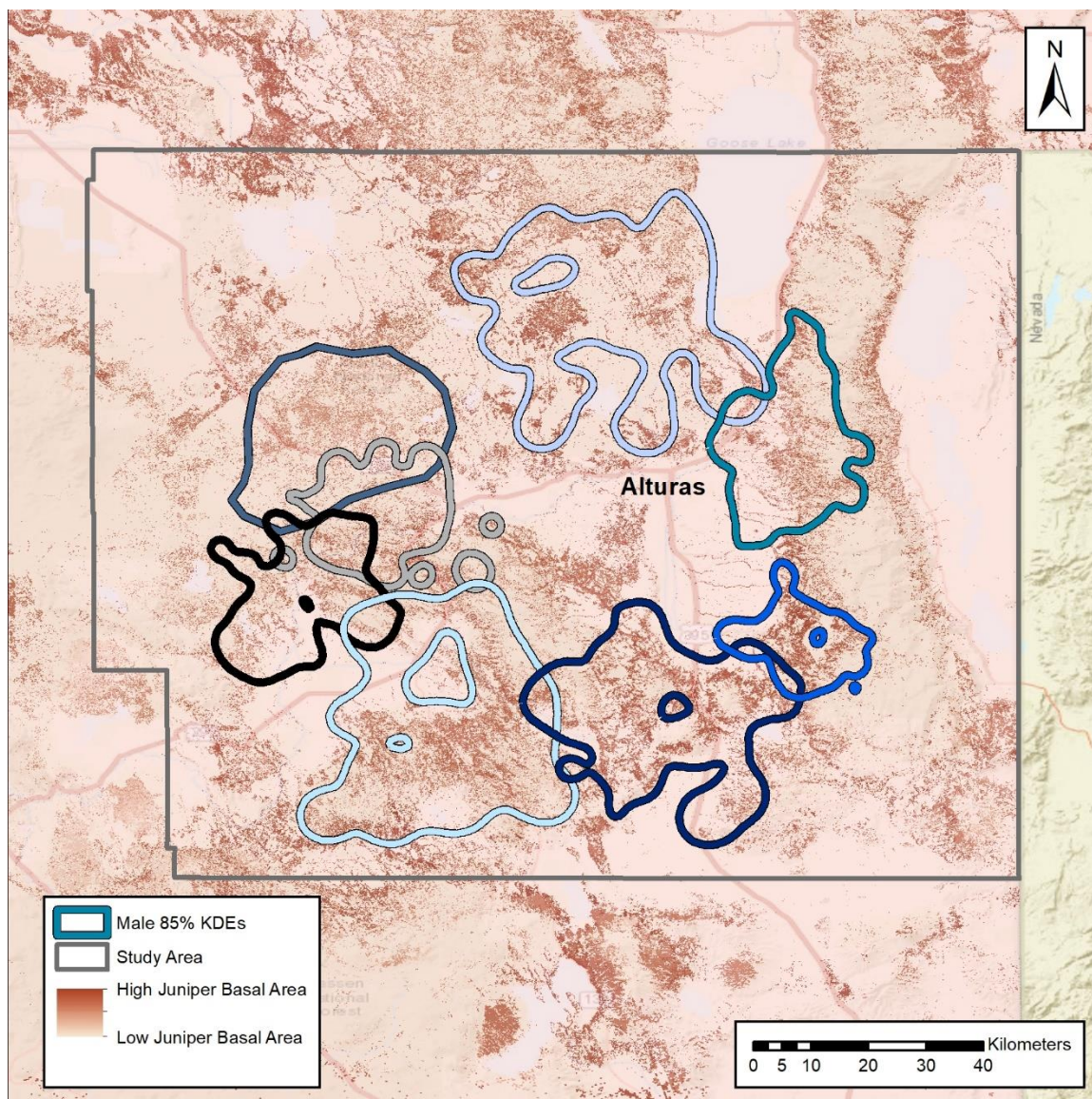


Figure B4. Male 85% kernel density estimates for GPS collared mountain lions in Modoc and Lassen counties, CA. Larger western juniper basal area is indicated by darker shades of red.

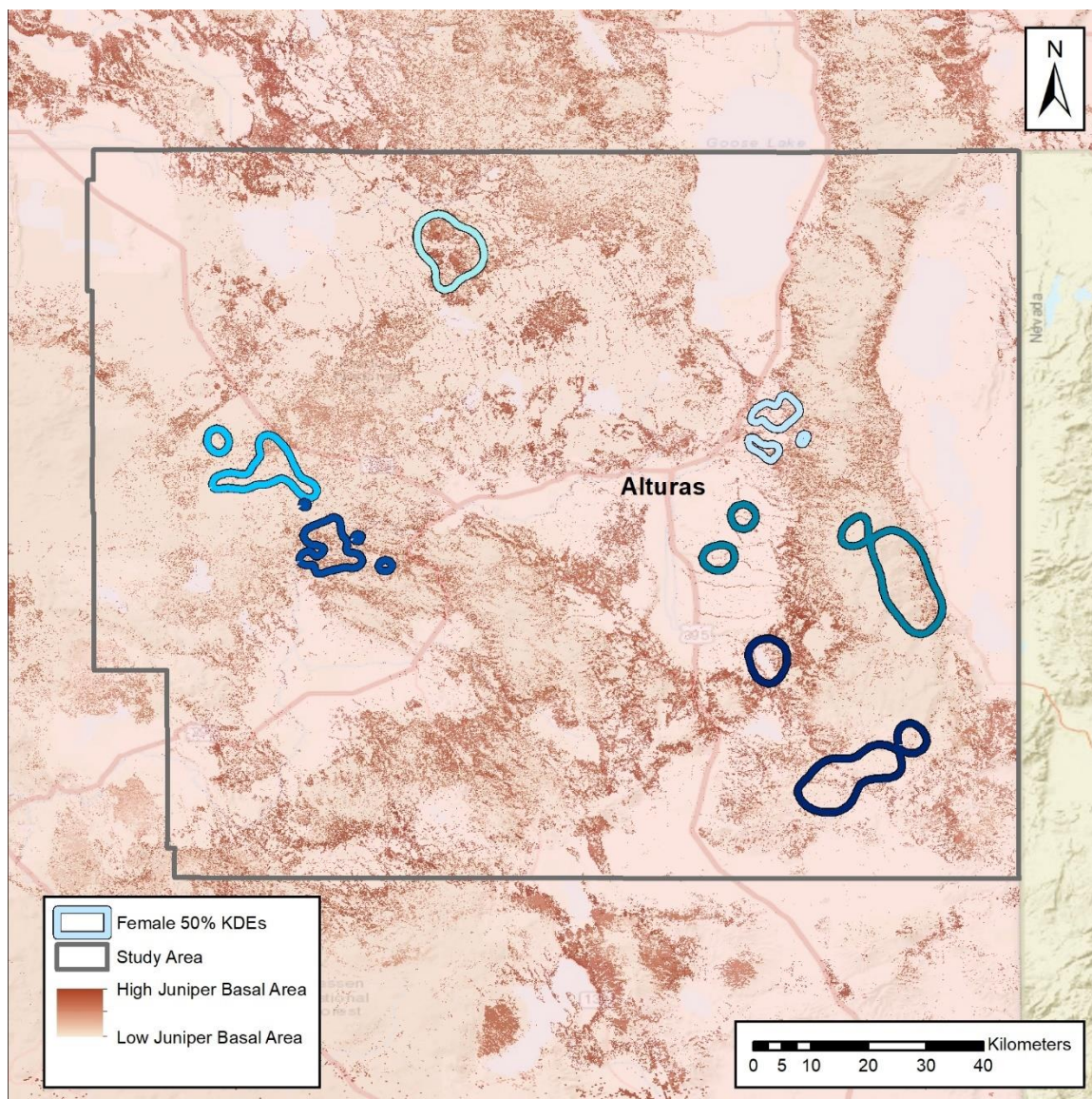


Figure B5. Female 50% kernel density estimates for GPS collared mountain lions in Modoc and Lassen counties, CA. Larger western juniper basal area is indicated by darker shades of red.

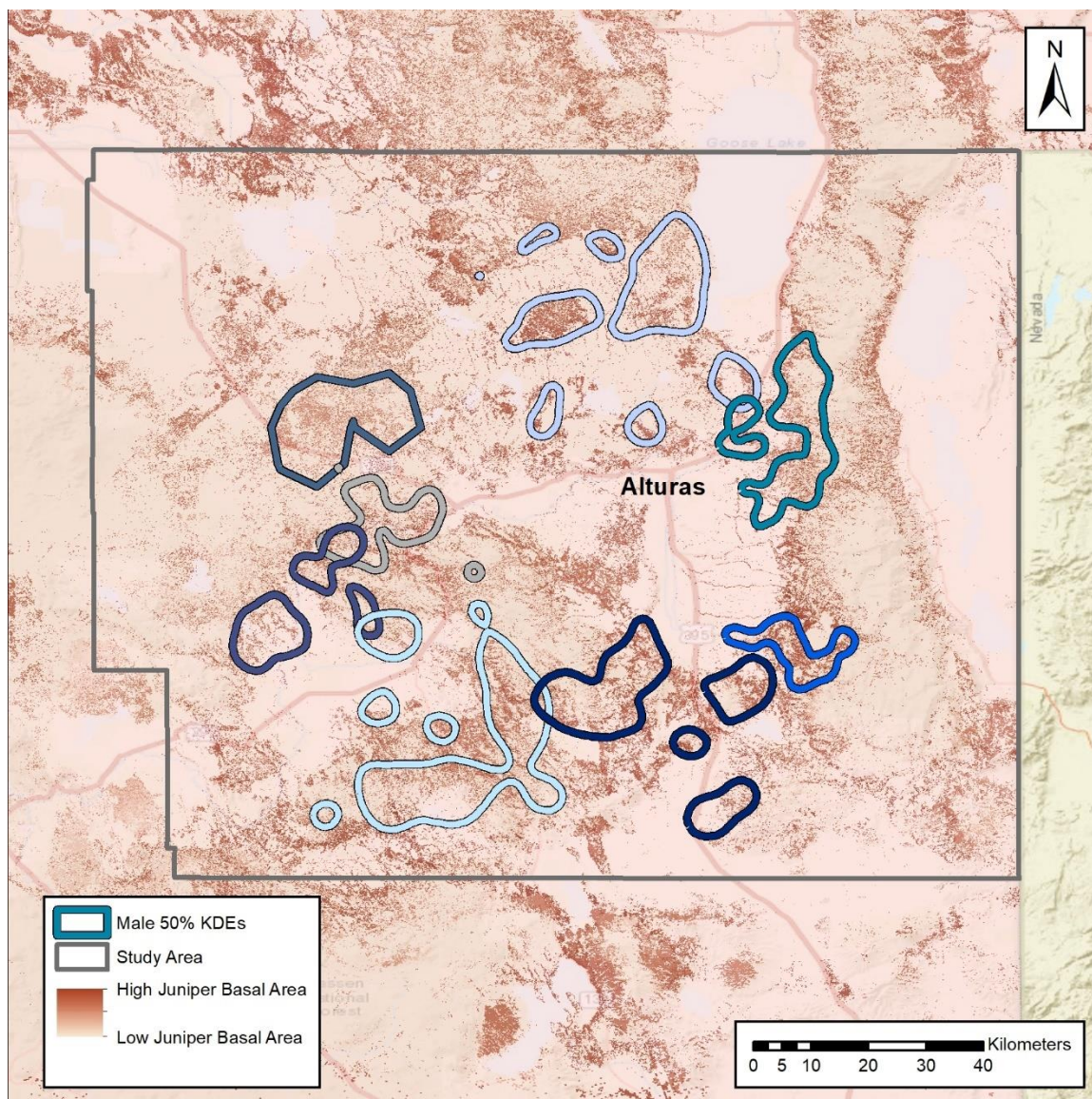


Figure B6. Male 50% kernel density estimates for GPS collared mountain lions in Modoc and Lassen counties, CA. Larger western juniper basal area is indicated by darker shades of red.

APPENDIX C

Appendix C: An Index of Similarity in Diets among Collared Individuals

A Morasita Horn Index of Similarity (Horn 1966) depicting how similar the diets were for each of the collared mountain lions in Modoc and Lassen counties, CA. Values of 1.0 indicate perfect similarity and values of 0 indicate no overlap in diets between study animals. Mountain lion ID numbers are on each of the axes, with F representing female and M representing male within the lion ID. Individual M166 is highlighted in green to highlight how dissimilar his diet was from the other lions. M166 preyed predominantly upon feral horses.

F158	1.00																
F159	0.77	1.00															
F163	0.84	0.94	1.00														
F164	0.88	0.96	0.95	1.00													
F180	0.72	0.99	0.91	0.94	1.00												
F182	0.72	0.99	0.91	0.94	1.00	1.00											
M157	0.81	0.97	0.98	0.96	0.95	0.95	1.00										
M160	0.84	0.72	0.86	0.80	0.67	0.67	0.81	1.00									
M161	0.85	0.98	0.96	0.98	0.96	0.96	0.97	0.77	1.00								
M166	0.01	0.00	0.00	0.04	0.00	0.00	0.00	0.08	0.01	1.00							
M168	0.72	0.99	0.91	0.94	1.00	1.00	0.95	0.67	0.96	0.00	1.00						
M178	0.66	0.61	0.66	0.72	0.59	0.59	0.67	0.55	0.63	0.01	0.59	1.00					
M179	0.77	0.98	0.92	0.95	0.97	0.97	0.98	0.72	0.97	0.01	0.97	0.68	1.00				
M181	0.18	0.20	0.24	0.20	0.18	0.18	0.22	0.22	0.20	0.00	0.18	0.13	0.19	1.00			
M184	0.65	0.54	0.66	0.63	0.51	0.51	0.61	0.78	0.59	0.00	0.51	0.59	0.55	0.16	1.00		
ID	F158	F159	F163	F164	F180	F182	M157	M160	M161	M166	M168	M178	M179	M181	M184		

Figure C1. A Morasita Horn Index of Similarity for the diets of GPS collared mountain lions in Modoc and Lassen counties, CA. Individual M166 is highlighted in green to emphasize how his diet differed from other study animals.

APPENDIX D

Appendix D: Prey Selection

The table below compiles data showing ungulate populations within the study area, in Modoc and Lassen counties, CA. Feral horse estimates were provided from the Modoc National Forest and were acquired by conducting aerial surveys. Mule deer, pronghorn and elk numbers were provided from California Department of Fish and Wildlife.

Population estimates were generated for each of the hunt units. These hunt units if Mule deer estimates were a combination of aerial surveys and road surveys. Pronghorn and elk estimates were based on aerial surveys conducted. Proportions of ungulates in the diet of mountain lions was based on GPS cluster investigations of 17 collared lions. The proportion is only representative of ungulates in the diet, all non-ungulate prey were removed.

Table D1. The proportion of ungulates available in the study area compared to proportions of ungulates observed in the diets of GPS collared mountain lions in Modoc and Lassen counties, CA.

Species	Population estimate	Number consumed	Proportion of ungulates available	Proportion of ungulates in diet
Mule deer	12362	163	70.15	79.90
Feral horses	2246	29	12.75	14.22
Pronghorn	1006	9	5.71	4.41
Elk	2007	3	11.39	1.47